# TAXONOMY OF ERIGERON SECT. POLYACTIS (COMPOSITAE: ASTEREAE)

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## ABSTRACT

Erigeron sect. Polyactis (Less.) Nesom is prominently characterized by arching-pendant buds, white ray corollas that sharply reflex at maturity and a pappus of 10-12 caducous bristles that break off cleanly at their very base. The bristles are completely absent in five species and usually replaced by a short, hyaline corona. The section is typified by E. delphinifolius Willd. and comprises 19 species, most of which are endemic to the Sierra Madre of western México. Nine new species are proposed here: E. annuactis, E. basaseachensis, E. caulinifolius, E. circulis, E. coroniglandifer, E. eruptens, E. nacoriensis, E. podophyllus and E. rhizomactis. One new combination is proposed: E. dactyloides (Greenm.) Nesom. The taxonomic history of the name of the section is presented. Achaetogeron A. Gray is included among the synonyms of Erigeron sect. Polyactis.

KEY WORDS: Erigeron, sect. Polyactis, Asteraceae, México, systematics.

The present study treats a monophyletic group of 19 species, which are formally described here as a section of *Erigeron*. Among these are taxa with a typical pappus of bristles as well as several that have only a low, coroniform pappus without bristles. The latter group includes *Achaetogeron wislizeni* A. Gray, the type of the genus *Achaetogeron* A. Gray.

#### STATUS OF THE GENUS ACHAETOGERON

Numerous Erigeron-like species with pappus bristles absent or reduced in various ways have been placed into Achaetogeron since its original recognition (Gray, 1849). Loss of pappus bristles in Erigeron, however, appears to have occurred independently in at least six lineages, and more than once in at least one of these (Nesom, unpublished). In addition to Erigeron wislizeni

(A. Gray) E. Greene, the following four species have pappus bristles absent or reduced and have been treated as Achaetogeron: E. galeottii (A. Gray ex Hemsl.) E. Greene, E. narcissus Nesom, E. gilensis Woot. & Standl. and E. coronarius E. Greene. Each of these species represents a separate lineage, each of which includes other epappose taxa. Further, E. strigosus Muhl. ex Willd. has ray achenes without bristles and could be considered to represent another lineage in which loss of bristles has occurred. I could find no features in plants of any of these lineages that would separate them from typical Erigeron (Nesom, 1980).

E.L. Greene (1891) was the first to make formal transfers of Achaetogeron species to Erigeron and a number of more contemporary botanists have commented on the probable congeneric status of the two genera (e.g., Shinners, 1946; De Jong & Longpre, 1963; Pinkava & Keil, 1977). I published a group of new names and new combinations that completed the transfer of Achaetogeron to Erigeron (Nesom, 1982). The present paper is the first to treat a monophyletic group of Erigeron species that includes both pappose

and epappose taxa.

# ERIGERON SECT. POLYACTIS - ITS NAME AND CHARACTERISTICS

With several seasons of field experience in species-rich southern Chihuahua, I feel reasonably confident in presenting this treatment of a monophyletic group of Erigeron species poorly or not at all represented in most herbaria. Only three of the new species proposed here are described from single collections of a taxon that I have not personally observed in the field. As noted in the discussions below, however, a number of problems remain. Further collecting and study in remote areas, particularly in northern Durango, will be necessary to clarify the taxonomy of Erigeron sect. Polyactis.

- Erigeron sect. Polyactis (Less.) Nesom, comb. et stat. nov. Based on Polyactis Less., Syn. Comp. 188. 1832; non Link, 1809. Type species: Erigeron delphinifolius Willd. Polyactidium DC, nom. nov., Prodr. 5:281. 1836.
- Stenactis Cass., Dict. Sci. Nat. 37:485. 1825. Type species: Erigeron delphinifolius Willd.; non sensu Less., 1832; non sensu Nees, 1832; non Erigeron sect. Stenactis (Cass.) Torr. & Gray, Fl. N. Amer. 2(1):172. 1841.
- Achaetogeron A. Gray, Mem. Amer. Acad. Arts, n. ser. 4(Pl. Fendl.):72. 1849. Type species: Achaetogeron wislizeni A. Gray.

When Cassini first formally described the new genus Stenactis in 1825, he cited three species as members, Erigeron (Aster) annuus (L.) Pers., E. delphinifolius and E. alpinus L. and stated that the description was drawn

from the first two. One of the characters that he emphasized as important in delimiting this group was the double pappus, but his description was also specific about the caducous nature of the pappus. Of the three species cited, only E. delphinifolius has a caducous pappus. The next year (Dict. Sci. Nat. 39:404. 1826), he removed E. annuus into a segregate genus, Phalacroloma Cass. Still later, in redescribing Stenactis (Dict. Sci. Nat. 50:483. 1827), he specifically stated that the description was drawn from E. delphinifolius, while including in the genus several more species with a double but non-caducous pappus. The species cited in 1827 as composing Stenactis primarily were the ones he had recognized in 1822 (Dict. Sci. Nat. 25:96) as sect. Diplopappus of the genus Diplopappus. However, in one of the first circumscriptions of Diplopappus (Dict. Sci. Nat. 13:308. 1819), Cassini formally cited four species, which are now recognized as Chrysopsis (D. lanatus and D. intermedius), Aster, and Erigeron annuus (D. dubius). Erigeron delphinifolius was mentioned in the 1819 discussion as a fifth species, but was not given a name as Diplopappus until 1822. Since he later removed both erigerons from this group, it is clear that the original reference of the name Diplopappus was to Chrysopsis or Aster and that the first supraspecific name for which E. delphinifolius is typical is Stenactis Cass.

Torrey & Gray's use of Stenactis at the sectional rank in Erigeron referred to six species that are not closely related to E. delphinifolius and none that were included among those cited by Cassini as belonging to Stenactis. Erigeron annus was moved by Torrey & Gray in the same publication to sect. Phalacroloma and E. alpinus to sect. Erigeron, although E. delphinifolius is a Mexican species and would not have been included in their floristic treatment. Later, however, Gray pointed out (Proc. Amer. Acad. Arts 8:648. 1873) that sect. Stenactis Torr. & Gray was a synonym of sect. Phoenactis Nutt. and that his own misapplication was based on the earlier misinterpretation of Stenactis by Nees & DeCandolle. In Gray's Synoptical Flora (1(2):219. 1884), he did not recognize Stenactis as a section, but he did correct his earlier concept of the name by noting Cassini's original association of Stenactis with E. delphinifolius and the close similarity of E. neomexicanus with that species. Because, however, the type species of Stenactis Cass. was excluded (see ICBN, Article 48.1) in the original publication by Torrey & Gray, sect. Stenactis should be attributed solely to those authors and cited as such, not as a new combination based on Cassini's genus.

Lessing's publication of the genus *Polyactis* was superfluous (as well as a later homonym), based on a misunderstanding of Cassini's work, since Lessing retained the genus *Stenactis* with the sole species *E. annuus*. DeCandolle corrected Lessing's creation of a later homonym, but *Polyactidium*, too, was superfluous, a synonym of *Stenactis*. Nees, like Lessing, used *Stenactis* to circumscribe a genus with *E. annuus* and several other species but did not

include E. delphinifolius. Polyactis, however, appears to be the first name typified by E. delphinifolius that is available for use at the rank of section.

Plants of sect. Polyactis are remarkably uniform in numerous aspects of their morphology. Almost all of the species produce pinnatisect leaves and the buds have a characteristic arching-pendant aspect that is easily recognized, even at a distance. The ray flowers are narrow and reflex sharply at the tube-ligule junction so that the corollas are held down around the involucre (this is often apparent even on herbarium specimens). The style branch (disc corolla) lengths and collecting appendage shapes are uniform. The pappus bristles, when present, are mostly 10-12 in number and the bristles have lateral constrictions at the very base, clearly perceptible with the SEM and break off there with only slight pressure. The achenes of some species are bristleless and usually have instead a hyaline corona or ring of partially fused scales or setae.

The behavior of the phyllaries is linked to the condition of the pappus, whether coroniform or of bristles. In those species with bristles, the phyllaries reflex or spread after maturation and release of the achenes; with an evolutionary loss of the bristles, the phyllaries remain erect, even after the achenes are dispersed. The reflexing behavior is more pronounced, however, in species of *Erigeron* with persistent rather than caducous bristles.

I know of no other species of Erigeron with the peculiar arching-pendant aspect of the buds nor of any with basally caducous pappus bristles. Reflexing ray corollas, however, are found in various other parts of the genus and I believe this feature is diagnostic in other species groups as well. In particular, in plants of the E. coronarius E. Greene group (including E. pumilus Nutt.), the ray corollas reflex and these species may be closely related to those of sect. Polyactis (Nesom, in prep.).

In the morphological descriptions that follow, all measurements were made from pressed specimens. Several types of trichomes, all multicellular, are found among the species treated here as well as the whole genus: (Type A) uniseriate, usually comprising the most conspicuous vestiture, described as hirsute, pilose, strigose, etc.; (Type B) uniseriate, very small and usually inconspicuous, not found to be of diagnostic value at the species level and not mentioned as such in the descriptions; (Type C) biseriate, glandular, described as "granular-glandular" in small size to "stipitate-glandular" when larger and capitate. Illustrations of these trichomes are found in Nesom (1976).

## Erigeron sect. Polyactis

Leaves commonly pinnately coarsely toothed or lobed, less commonly entire, the mid-region of the blade oblong and of even width. Heads shallowly hemispheric to cupulate, markedly impressed below, buds arching-pendant;

phyllaries linear-lanceolate, with whitish but usually not scarious lateral zones, in 3-4(-5) series of nearly equal length, but the inner often shorter than the outer, reflexing to spreading after achene maturation and release in the species with a pappus of bristles, remaining erect if pappus coroniform; receptacles flat to convex, smooth or alveolate. Ray flowers 50-230 in 2-4 series, corollas 5-16 mm long, the ligules 0.6-1.2 mm wide, white and drying white or sometimes cyanic in several species, sharply reflexing at the tube-ligule junction at maturity. Disc corollas narrowly tubular-funnelform, 1.8-4.0 mm long, the tube slightly constricted, barely or not at all inflated or indurated above the constriction; style branches 0.4-0.7 mm long, including the deltate to narrowly triangular collecting appendages 0.1-0.2 mm long. Achenes compressed, mostly oblong-oblanceolate, (0.8-)1.0-1.3(-1.8) mm long; pappus of mostly 10-12 (11-17 in E. podophyllus) brittle, basally caducous bristles, or the bristles absent and replaced by an outer corona or series of scales, usually basally fused, 0.1-0.2(-0.5) mm high. Chromosome number, n=9, 18 pairs.

All the species of Erigeron sect. Polyactis occur in the western Sierra Madre of México. Thirteen species of sect. Polyactis are known only from Chihuahua, Sonora and Durango. Two of them, E. neomexicanus and E. oreophilus, range into the southwestern United States and the type species, E. delphinifolius, has the major part of its range in the trans-volcanic mountains of south-central México. Most occur above 1700 meters and are found primarily in oak to oak-pine or pine woodlands but sometimes range into associated grasslands. Erigeron neomexicanus and E. oreophilus occur as low

The most significant differences among the species of sect. Polyactis are in the type of pappus (coroniform or bristles) and the presence or absence of rhizomes, stipitate-glandular trichomes and clasping leaves. Erigeron polycephalus and E. annuactis have a distinctive leaf shape different from other species. Comments on possible interspecific relationships follow individual descriptions, but there is not sufficient basis for attempting to outline a hypothesis of phylogeny for all the species.

I do believe, however, that the species of Erigeron sect. Polyactis with a coroniform pappus (vs. pappus of bristles) comprise a distinct lineage. This switch in pappus morphology apparently has entailed not only loss of the bristles, but the elaboration of a corona, which is a structure probably derived from the "outer" series of setae or scales. See the comments following

E. coroniglandifer for a caveat regarding this hypothesis.

## SPECIES TAXONOMY Artificial key to the species of sect. Polyactis

1.	Achenes	with	a core	oniform	pappus,	without	bristles	 (2	,
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	2. Cauline leaves clasping or subclasping
	2. Cauline leaves not at all clasping(4)
3.	Plants producing slender, scale-leaved rhizomes; upper stem pubescence appressed, eglandular E. rhizomactis
3.	Plants without rhizomes; upper stem pubescence spreading, usually prominently stipitate-glandular E. coroniglandifer
	4. Basal leaves strongly bipinnatifid, produced at tips of slender rhizomes; cauline leaves of erect stem ca 35; heads 6 mm wide; phyllaries 2.5-3.0 mm long E. circulis
	4. Basal leaves entire to toothed or lobed, never strongly bipinnatifid; cauline leaves 10-30; heads 7-17 mm wide; phyllaries 3.1-5.5 mm long
5.	Phyllary margins thick, whitish; rays 115-180; pappus a corona 0.2-0.5 mm high, with an erose or scaly margin; receptacles alveolate E. wislizeni
5.	At least the inner phyllaries with relatively broad, hyaline margins; rays 40-230; pappus a blunt, cartilaginous rim less than 0.05 mm high; receptacles punctate to very shallowly alveolate E. griseus
	6. Plants annual
	6. Plants perennial(9)
7.	Stems, leaves and phyllaries stipitate-glandular; leaves clasping to sub- clasping E. inoptatus
7.	Plants eglandular or the phyllaries sometimes minutely granular-glandular; leaves not at all clasping
	8. Cauline leaves pinnatifid to bipinnatifid E. delphinifolius
	8. Cauline leaves entire E. annuactis
9.	Cauline leaves clasping to subclasping
9.	Cauline leaves not at all clasping(11)
	10. Stems eglandular, appressed-strigose at least near the heads; cauline leaves obovate to oblong-obovate, the midregions elliptic E. caulinifolius
	10. Stems stipitate-glandular, hirsute-pilose; cauline leaves oblong-oblanceolate to oblong-lanceolate, the midregions narrowly oblong E. seemannii
1	1. Leaves serrate or crenate, the blades elliptic to elliptic- oblanceolate; capitulescence corymbose E. polycephalus

	oblong to oblong-lanceolate; heads solitary or in a loosely corymbose capitulescence
	12. Plants mostly 25-90 cm tall; stems usually with 2-20 primary branches, these often with secondary and tertiary branches (13)
	12. Plants mostly 10-30 cm tall; stems unbranched or with 1-2 simple branches
13.	Stems, leaves and phyllaries moderately to densely appressed-strigose to hirsute with trichomes averaging 0.4 mm long, eglandular or sometimes minutely glandular on the phyllaries E. neomexicanus
13.	Stems, leaves and phyllaries sparsely hispid-pilose with trichomes averaging 1.0 mm long, often the whole plant but at least the peduncles and phyllaries densely stipitate-glandular
	14. Leaves deeply pinnatifid with lobes evenly distributed along the margins E. oreophilus
	14. Leaves coarsely toothed or lobed only on the distal half, the blades with a broad midregion of even width E. dactyloides
15.	At least the peduncles and upper leaves prominently stipitate- glandular E. oreophilus
15.	Peduncles and upper leaves hairy, sometimes granular-glandular, but never stipitate-glandular(16)
	16. Inner and outer phyllaries with broad, scarious margins E. subacaulis
	16. Inner phyllaries indurated to the edge or with a minute, hyaline rim
17.	Cauline leaves entire, apically toothed, or reduced to bracts on essentially scapose stems
17.	Cauline leaves pinnatifid(20)
	18. Plants with thick, lateral rhizomes; basal and lower cauline leaves 7-18 mm wide, 10-35 mm long, with 1-3(-4) pairs of coarse, apical teeth or shallow lobes; pappus bristles 11-17 E. podophyllus
	18. Plants with ascending caudex branches, not rhizomatous; basal leaves pinnatifid; pappus bristles 10-12(-14)
19.	Stems and phyllaries eglandular; cauline leaves 2-10 mm wide, 10-26 mm long, entire or shallowly toothed, reduced to bracts near the head heads 5-7 mm wide: disc corollas 2.4-3.0 mm long E. nacoriensis

11. Leaves pinnatifid, less commonly coarsely toothed, the blades mostly

- 19. Stems and phyllaries glandular; cauline leaves absent or completely bracteate (the stems scapose); heads 8-15 mm wide; disc corollas 3.5-4.5 mm long ...... E. eruptens
  - 20. Plants mostly 10-30 cm tall, producing slender, brittle, lateral rhizomes; basal rosette present at flowering; heads 6-9 mm wide; ray flowers 35-63 ...... E. basaseachensis
  - 20. Plants mostly 25-90 cm tall, without rhizomes; basal rosette usually absent at flowering; heads 7-12 mm wide; ray flowers 70-150 ...... E. neomexicanus

Erigeron annuactis Nesom, sp. nov. Type: MÉXICO, Michoacán: Mpio. Uruapán, Cascadas de Tzararacua, [ca 10 km] S of Uruapán of Hwy 37, [19° 40'N, 102° 13'W], pine-oak woods, 1400 m, 16 Dec 1984, C. Cowan 4866 (holotype: TEX!; isotype: MEXU [not seen]).

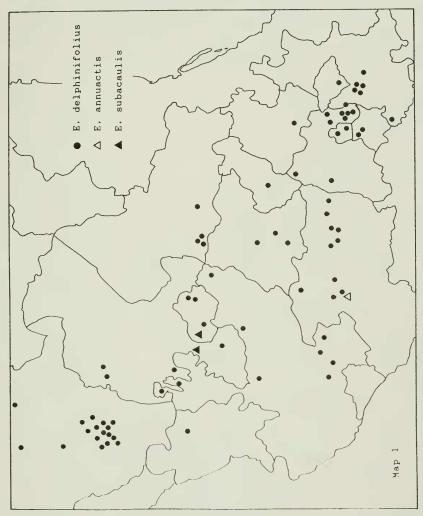
E. delphinifolio Willd. similis sed foliis penitus integris plerumque 3plo longioribus quam latioribus et corollis radii brevioribus et paucioribus differt.

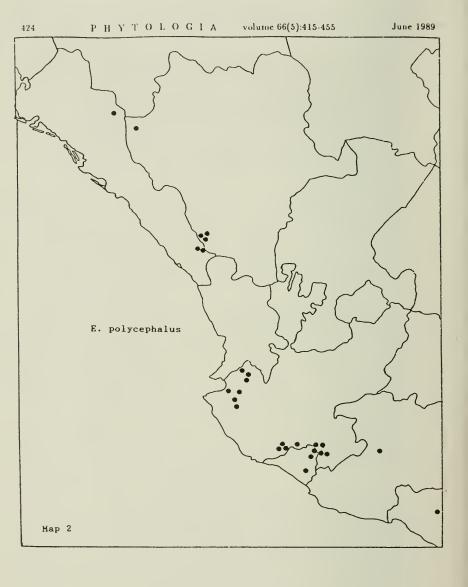
Annuals 6-7 dm tall. Stems with numerous branches on the upper 1/2-1/3, sparsely short-strigose, eglandular, ridged-striate. Mid-cauline leaves minutely strigose, elliptic-ovate to elliptic-obovate, 40-50 mm long, 13-16 mm wide, mostly 3 times longer than wide, epetiolate, entire, not even mucronulate, not clasping, the upper cauline leaves narrowly elliptic to ovate or lanceolate-ovate, 2.5-4.0 mm wide, 7-12 mm long. Heads 6-8 mm wide, on peduncles 3-35 mm long; phyllaries 3.0-3.5 mm long, densely minutely granular-glandular, without other vestiture or the outermost with a few small and very inconspicuous hairs. Ray flowers 85-110 in 2-3 series, the corollas 5.5-6.2 mm long, 0.8-1.0 mm wide. Disc corollas 3.0-3.3 mm long, indurated and slightly inflated above the constriction. Achenes 0.8-0.9 mm long, sparsely strigose; pappus of 8-10 bristles, without an outer series.

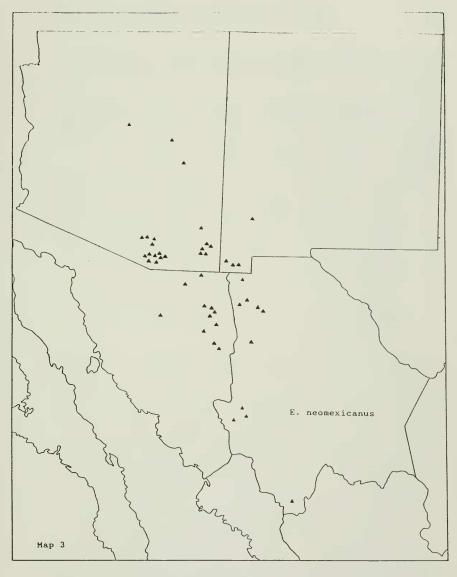
Known only from the type collection. Map 1.

Erigeron annuactis is represented by the top half of a single plant, but Cowan's label notes that it was an annual. It is obviously similar to E. delphinifolius in duration and the structure of its capitulescence, but the relatively broad, completely entire leaves are strikingly different from the pinnatifid or bipinnatifid leaves of the latter. Further, in E. delphinifolius the upper cauline leaves are reduced to linear bracts (even these often deeply obed) 0.5-1.2 mm wide, mostly 10-16 times longer than wide.

Erigeron annuactis is the only entire-leaved taxon in the section; the leaf hape in this species is closest to that of E. polycephalus, although the latter isually has toothed leaves and is strongly perennial. I believe these two, with Z. delphinifolius, which share corymbose capitulescences with relatively







short-peduncled heads, probably constitute a distinct lineage within the section. It is not clear to which of these *E. annuactis* may be most closely related.

Erigeron annuactis occurs at the southern periphery of the range of both E. delphinifolius and E. polycephalus and collections of both of the latter have been made from the vicinity of Uruapán: E. delphinifolius, all with typically deeply pinnatifid leaves (Tancitaro, Hinton 15556; 8 km S of Uruapán, King & Soderstrom 4773; E. polycephalus (Uruapán, Woronow 2916).

Erigeron basaseachensis Nesom, sp. nov. Type: MÉXICO, Chihuahua: Mpio. Ocampo, ca 2.5 km S of village of Basasaeachic, area of La Cascada de Basaseachic, 28° 02'N, 107° 55'W; area of pine-oak-juniper-manzanita woodlands between parking area and top of falls; abundant in crevices of steep, W-facing rock walls and shallow soil pockets in boulders along river near falls, 18 Aug 1984, G. Nesom 5089 with P. Lewis (holotype: TEX!; isotypes: ARIZ!, ASU!, CAS!, CIIDIR!, COLO!, ENCB!, F!, GH!, MEXU!, NMC!, NY!, RM!, US!).

Ex speciebus sectionis *Polyactis* statura plerumque parva, rhizomatibus tenuibus ligneis, vestimento eglanduloso, caulibus nonramosis ascendentibus ad basim, et capitulis solitariis in pedunculis longis distinguenda.

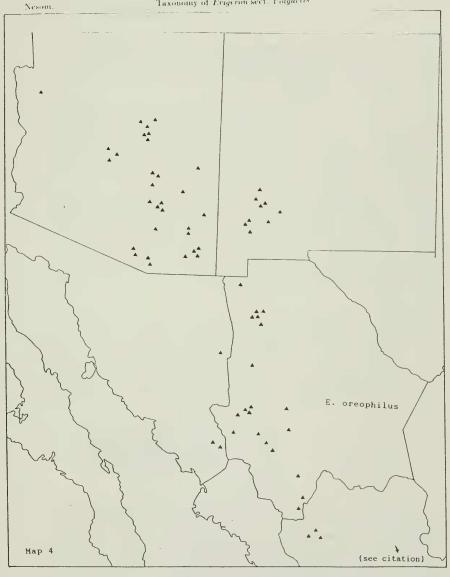
Herbaceous perennials from fibrous roots, producing short, slender, brittle rhizomes. Stems basally ascending, (8-)10-30 cm tall, usually unbranched or with 1-2 short, simple branches near the middle, sparsely pubescent with antrorsely ascending to appressed hairs, eglandular. Leaves sparsely but coarsely strigose, eglandular, the basal in a rosette, pinnatifid with 1-3 pairs of obovate (to linear) lobes, 15-55(-75) mm long, 5-15 mm wide (lobe tip to tip), petiole ca half the leaf length; the cauline reduced in size, nonclasping, sessile, quickly becoming entire and oblanceolate. Heads solitary, 6-9 mm wide, on naked peduncles 2.5-10.0 cm long; phyllaries sparsely strigosehirsute, eglandular, 3-4 mm long. Ray flowers 35-63 in a single series, the corollas white, drying white to pinkish-purple, 7.0-9.0 mm long. Disc corollas 2.0-3.5 mm long. Achenes 0.9-1.2 mm long, sparsely strigose; pappus of (9-)10-12 very slender, basally caducous bristles, with a prominent outer series of very slender, lanceolate to oblong scales 0.1-0.3 mm high.

Apparently endemic to the area of the confluence of Rio Candameña and Rio Durazno south of Basaseachic in southwestern Chihuahua; on the plateau primarily in areas of pine and pine-oak woods, N and W-facing cliff crevices and shallow soil pockets in boulders alongside the river, rarely in sandy soil of floodplain (2050-2100 m), and on wet rocks and cliffs at base of the falls

(ca 1800 m); flowering August-October. Map 5.

Additional collections examined: MÉXICO, Chihuahua: [Type locality]: banks of small stream entering Rio Candameña, near wooden footbridge on





trail to falls, 17-20 Oct 1986, Nesom 5536 (TEX,MEXU); beside Río Durazno, 17-20 Oct 1986, Nesom 5609 (MEXU,NMC,TEX); base of falls, 14 Oct 1984, Spellenberg 7935 (NMC,TEX); plateau above falls, 14 Oct 1984, Spellenberg 7912 (TEX).

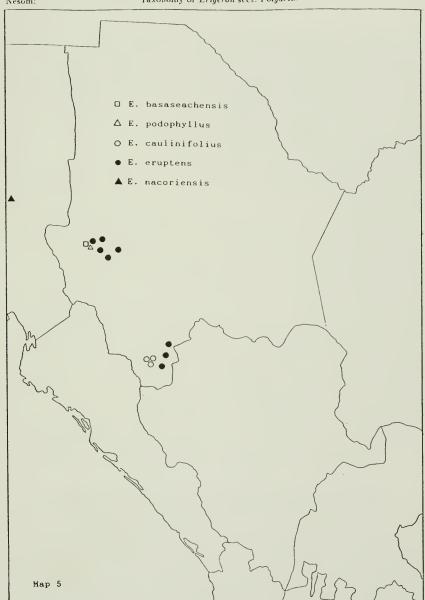
The plants of the type collection are similar to those collected by Spellenberg. Those of Nesom 5536 have slightly longer stems (to 40 cm long) and the cauline leaves are unreduced or slightly enlarged from the basal. However, the stems appear to have regrown from a point below where the original ones had been broken off. They are otherwise identical to the typical plants and are probably aberrant growth forms.

Erigeron basaseachensis is distinguished from all the species of sect. Polyactis by its combination of small size, slender, woody rhizomes, sparsely strigose, eglandular vestiture, mostly unbranched, basally ascending stems and solitary heads on long peduncles. In the area of Basaseachic, it is similar to E. neomexicanus which differs in its larger stature, lack of rhizomes, spreading stem pubescence (in the Basaseachic area) of much coarser hairs, basal leaves usually absent by flowering, loosely corymbose capitulescence borne on stems branched in the upper third and fewer ray flowers on mostly smaller heads.

Erigeron caulinifolius Nesom, sp. nov. Type: MÉXICO, Chihuahua: Mpio. Guadalupe y Calvo, NW side of Cerro Mohinora, ca 12.5 mi SW of Guadalupe y Calvo, past turnoff to peak, downslope on road toward Sinaloa; 25° 57'N, 107° 03'W; abundant on cliff faces, in area of oakpine-fir and scattered madroños, 2470 m, 20 Aug 1988, G. Nesom 6483a with A. McDonald (holotype: TEX!; isotypes: ARIZ!, CIIDIR!, COLO!, GH!, MEXU!, MICH!, MO!, NMC!, NY!, RM!, US).

Ex affinitate sect. *Polyactis* distinguenda caulibus pubescentia supera appressa infera patenti, foliis caulium amplis obovatis vel oblongi-obovatis grosse serratis prope apices amplectentibus non-ampliatis ad bases, capitulescentiis laxe corymbosis, capitulis in pedunculis brevibus, et pappo setis.

Perennial herbs from a short caudex, producing numerous fibrous roots, sometimes with a short (2-5 cm), thickened rhizome. Stems 30-55 cm tall, with 4-8(-12) branches on the upper half, often with secondary branches, pubescence sparsely spreading to spreading-deflexed pubescence on the lower 2/3-3/4, appressed-strigose near the heads, eglandular. Leaves sparsely to moderately strigose, eglandular, the basal ovate-elliptic, 5-15 cm long, serratedentate to somewhat lyrate with 5-10 pairs of coarse teeth or basal lobes, basally attenuate to a petiole 1/3-1/2 the leaf length; cauline leaves obovate to oblong-obovate, often widely so, oblong-lanceolate in the capitulescence,



the middle 32-85 mm long, 9-25 mm wide, coarsely serrate to dentate-serrate on the distal 1/2-2/3, clasping to subclasping but not basally ampliate. Heads in a loosely corymbose capitulescence, 11-13 mm wide, on peduncles 15-35 mm long; phyllaries 4.5-6.0 mm long, sparsely strigose-hispid, sparsely stipitate-glandular. Ray flowers 125-180 in 2-3 series, the corollas white, 11-16 mm long. Disc corollas 3.0-3.5 mm long. Achenes with 2(-3) orange nerves, sparsely strigose, mature size not observed; pappus of 10-12 slender, brittle and basally caducous bristles slightly shorter than the disc corollas, with an outer series of minute, slightly basally fused scales 0.1 mm high.

Known only from the area of Cerro Mohinora in southern Chihuahua; steep, rocky faces and roadbanks, area of pine-oak-fir; 2450-3100 m; Aug-

[Oct]. Map 5.

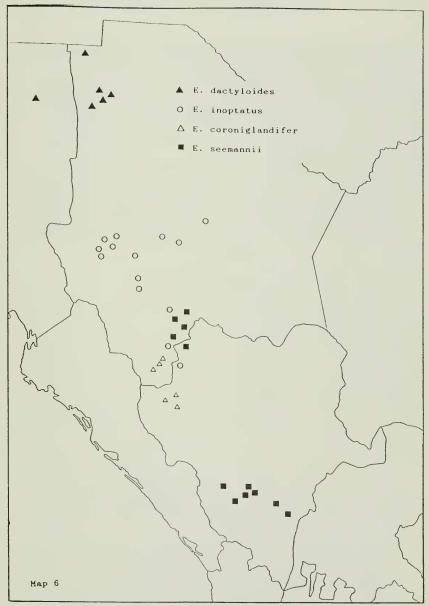
Additional collections examined: MÉXICO, Chihuahua: Mpio. Guadalupe y Calvo, Cerro Mohinora, bosque conifero, 3100 m, 27 Aug 1987, McDonald 2412 (TEX); NE side of Cerro Mohinora, ca 2 mi below summit, ca 11 mi SW of Guadalupe y Calvo, steep, rocky roadbank in pine-fir-aspen woods, 2610 m, 21 Aug 1988, Nesom 6481 with McDonald (MEXU,TEX).

Erigeron caulinifolius is distinct among all the species of sect. Polyactis in its very large, coarsely toothed, obovate to oblong-obovate, and clasping but not basally ampliate cauline leaves. Other distinguishing features of this species are the following: stem pubescence spreading to deflexed on the lower 3/4, appressed-strigose above, otherwise eglandular, heads on short peduncles in a loosely corymbose capitulescence and pappus of bristles. It is similar to and perhaps most closely related to E. seemannii but the latter has stem pubescence spreading from bottom to top, leaves with narrowly oblong midregions and densely stipitate-glandular stems, leaves and phyllaries.

Erigeron circulis Nesom, sp. nov. Type: MÉXICO, Chihuahua: La Rocha, along tributary of Río del Soldado, on N-facing conifer slope, Sierra Mohinora, [ca 26° 07'N, 107° 03'W], 7500 ft, 14-15 Oct 1959, D.S. Correll & H.S. Gentry 23122 (holotype: LL!).

E. delphinifolio Willd. similis pubescentia caulium appressa, foliis basalibus bipinnatisectis, et foliis caulium non-amplectentibus sed rhizomatibus brevibus, foliis caulium integris, capitulis solitariis minoribus, flosculis minoribus, et pappo sine setis differt.

Perennial herbs from fibrous roots, producing slender rhizomes, ascending at the tips and producing a rosette of leaves. Erect stem 31 cm tall, moderately strigose with closely appressed to ascending hairs, eglandular. Leaves sparsely strigose, eglandular, the basal 3-4 cm long, the blades widely obovate in outline, 12-19 mm wide, bipinnatifid with 3-4 pairs of primary oblanceolate lobes, the sinuses extending 9/10 of the distance to the midrib, secondary lobes much shallower, the cauline 35 in number, 20-40 mm long,



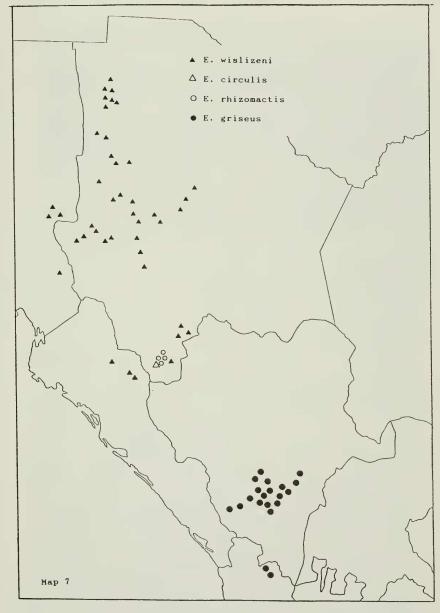
3-5 mm wide, narrowly oblong to lanceolate, epetiolate, not clasping, entire or with 1-2 shallow teeth near the apex, unreduced in size until the peduncle, the uppermost reduced to linear bracts. Head 6 mm wide, solitary on a peduncle 7 cm long; phyllaries in 2-3 subequal series, the inner 3.0 mm long, the outermost 2/3 as long, very sparsely strigose, eglandular, Ray flowers ca 70 in 2-3 series, the corollas white, 7-11 mm long. Disc corollas 1.9-2.7 mm long. Achenes with 2 (thin?) ribs, sparsely strigose, mature size not observed; pappus a ring of irregular scales or a fimbriolate corona less than 0.1 mm high.

Known only from the type collection. Map 7. The site at La Rocha was on the northeastern slope of Cerro Mohinora (Correll, 1959). Correll noted that the collecting site was along the tributary of Rio del Soldado in a gorge facing southwest with "flumes and miniature fall" cut by the stream and "sheltered by a dense forest of balsam and pine. Sheltered in this fern paradise were found 23 species of ferns, 6 of which were new to the known flora of Chihuahua." Correll described his experience there as "one of the thrills of a lifetime."

Erigeron circulis is characterized by slender rhizomes, appressed stem pubescence, very small, deeply dissected, bipinnatifid basal leaves, mostly entire, non-clasping cauline leaves, small solitary heads with small flowers and achenes lacking a pappus of bristles. The coroniform pappus clearly places it as a member of the E. wislizeni group, but the only other plants in the section with such highly dissected leaves are forms from Durango of E. delphinifolius, with which it is compared in the diagnosis. In the area of Cerro Mohinora, E. rhizomactis also has slender rhizomes and a coroniform pappus, but it has many different features, including mostly entire to fewtoothed basal leaves, clasping cauline leaves and much larger heads with longer and more numerous ray flowers and longer disc corollas. Plants of E. wislizeni have neither such dimorphic leaves (basal vs. cauline) nor slender rhizomes.

The plant of *Erigeron circulis* is mounted on a sheet with three plants of *E. strigulosus* E. Greene. The latter is in a different section of the genus and prominently different from *E. circulis* in many ways, including its lack of rhizomes, spreading stem pubescence, entire leaves, clasping cauline leaves and more numerous ray flowers with coiling ligules.

Erigeron coroniglandifer Nesom, sp. nov. Type: MÉXICO, Chihuahua: Mpio. Guadalupe y Calvo, 1.3 km S of bridge in Turuachi near base of steep canyon, 78.9 km SW of El Vergél, 26° 09'N, 106° 44'W; area of pine-oak and madroño, 2050 m, plants abundant in shallow soil over steep, rocky slope, 28 Aug 1983, G. Nesom 4964 (holotype: TEX!; isotypes: ARIZ!,ASU!,CAS!,CHAPA!,CIIDIR!,COLO!,ENCB!,F!, GH!,K!, M!,MEXU!,MO!,NMC!,NY!,RM!,US).



E. seemannii (Schultz-Bip. ex Seem.) E. Greene similis sed pappo hyalino coroniformi sine setis differt.

Perennial herbs, producing fibrous roots from a very short, thick rhizome. Stems 25-46 cm tall, simple or with 2-5 branches from near the middle or somewhat above, sparsely to densely hispid-pilose from bottom to top, sometimes slightly deflexed, densely and prominently stipitate-glandular or sometimes the glands smaller and relatively inconspicuous. Basal leaves pinnately lobed or toothed, usually deciduous by flowering, the lower cauline narrowly oblong to oblanceolate, coarsely toothed to shallowly lobed on the distal half, with a broad midregion of even width, becoming lanceolate and entire or nearly so upwards, the largest 4-7 cm long, 5-18 mm wide, 4-10 times longer than wide, little reduced in size until the peduncles, mostly sessile with clasping to subclasping, slightly ampliate bases, stipitate-glandular and sparsely hispid. Heads 9-15 mm wide, on naked peduncles 7-15 cm long; phyllaries very sparsely to densely hispid-pilose, prominently stipitate-glandular. Ray flowers 115-225 in 2-3 series, corollas white, sometimes drying with a lilac tinge, 7.0-8.5 mm long. Disc corollas 2.2-3.0 mm long. Achenes 1.0-1.3 mm long, with 2, thickish, white ribs, glabrous to very sparsely strigose; pappus a thin, hyaline, erose-margined corona 0.05-0.1 mm high.

Northern Durango and southern Chihuahua; rocky habitats in areas of pine-oak woods; 2050-2700 m; Jul-Sep. Map 6.

Additional collections examined: MÉXICO, Chihuahua: Mpio. Guadalupe y Calvo, 16 km S of bridge in Turuachi near top of road upgrade through canyon from Turuachi, ridge overlooking town of Yerbitas, 0.5 km S of Guadalupe y Calvo-Atascaderos jct, 2600 m, abundant on dry, rocky slope, 26 Aug 1983, Nesom 4978 (TEX); ca 13 mi E of Guadalupe y Calvo, 4.5 mi W of jct to Atascaderos, clearing in pine-oak woods, 2700 m, 24 Aug 1984, Nesom 5147b (TEX). Durango: Mpio. Santiago Papasquiaro, ca 22 air mi WNW of Santiago Papasquiaro, 3.3 mi by Topia Rd W of the sierra crest from jct with road to antenna, crest of mountain with pine and oak, ca 8750 ft, 25 Aug 1983, Corral & Worthington 11445.5 (TEX); [Mpio. Canelos], [ca 35 km SE of Topia], ca 100 mi NW of Santiago Papasquiaro, 11 mi E of Cienega Nuestra Señora, 19 Sep 1982, Spellenberg & Zimmerman 6764 (NMC,TEX); Mpio. Tepehuanes, "Buenos Aires," 36 km W of Tepehuanes, [por la brecha a] Topia, pine-oak woods, 22 Jul 1982, Tenorio L. 1187 (TEX).

Erigeron coroniglandifer is very similar to E. seemannii in its perennial habit, stipitate-glandular stems, leaves and phyllaries, its long, naked peduncles, completely spreading stem pubescence and clasping leaves with broad midregions. The latter, however, has a pappus of caducous bristles with no outer series. Erigeron coroniglandifer completely lacks bristles but has a hyaline corona. It apparently is restricted to the high mountains and plateaus of northwestern Durango and extreme southern Chihuahua; no populations of

E. seemannii have been found in that area. Erigeron seemannii has a wider distribution from south-central Durango to southern Chihuahua. Although the morphological difference between the two taxa is small, it is striking and accompanied by geographic differentiation. The close similarity between the two species suggests that E. coroniglandifer may be derived directly from E. seemannii, in which case the former would be a high-elevation isolate, probably similar in origin to that of E. rhizomactis from E. wislizeni. If the difference between a coroniform pappus and one of bristles, however, is more basic (see comments in Introduction), E. coroniglandifer may be closely related to the E. wislizeni group.

Erigeron dactyloides (Greenm.) Nesom, comb. nov. Based on Erigeron oreophilus var. dactyloides Greenm., Proc. Amer. Acad. Arts 41:258. 1905. Type: MÉXICO, Chihuahua: [Mpio. Casas Grandes], near Colonia Garcia in the Sierra Madre, 1-20 Aug 1899, E.W. Nelson 6220 (lectotype designated here: GH!; isolectotype: US!).

Perennials, with stems, leaves, peduncles and phyllaries stipitate-glandular, the glands larger and denser on the upper part of the plants. Stems erect, ca 0.6-1.0 m tall, glandular and sparsely hispid-pilose, Leaves (mid-cauline) not clasping, 5-8 cm long, oblong to oblong-oblanceolate, 8-12 mm wide, narrowing slightly near the tip, of nearly uniform breadth in the proximal 1/2-2/3, with 1-2(-7) pairs of shallow lanceolate lobes on the distal margins, often with 3, prominent longitudinal veins, entire, more lanceolate and somewhat reduced in size on the upper portions of the stem. Heads 8-10 mm wide, in a leafy capitulescence; phyllaries densely stipitate-glandular but with few other hairs. Ray flowers 140-160. Disc corollas 2.7-3.0 mm long. Mature achenes not seen; pappus of 10-12 bristles, with a distinct, outer series of triangular-lanceolate scales 0.1 mm high.

Northwestern Chihuahua and adjacent Sonora; rocky sites in oak-pine woods; 2250-3000 m; Aug-Oct. Map 6.

Additional collections examined: MÉXICO, Chihuahua: E side of San Luis Mts, 11 Sep 1893, Mearns 2232 (CAS); Strawberry Creek, NE of Colonia Pacheco, 22-24 Sep 1934, Pennell 19172 (US); cool slopes, foothills of the Sierra Madre, 11 Oct 1887, Pringle 1272 (GH,MEXU,MICH,PH,US); near Colonia Garcia in the Sierra Madre, 4 Sep 1899, Townsend & Barber 305 (GH,MEXU,MICH,MO,NMC,UC,US), 306 (MEXU); ca 25 mi W of Colonia Juaréz on road to Colonia Pacheco, 20 Sep 1981, Warnock 2334 (TEX). Sonora: Cañon Internacional, oak-pine zone, 23 Aug 1940, White 3507 (MEXU,MICH).

I earlier maintained this taxon as a variant of *E. oreophilus* (Nesom, 1980) but now consider it to be distinct at the rank of species. *Erigeron dactyloides* has larger, oblong leaves with 1-3 teeth or small lobes on the upper 1/2-2/3 of the blade and a broad midregion of even width, commonly with three

longitudinal veins. In contrast, over its whole geographic range, the leaves of *E. oreophilus* are generally smaller and consistently deeply pinnatifid with lobes evenly spaced along the margins. Additionally, *E. dactyloides* appears to be restricted to a relatively small area in northwestern Chihuahua and adjacent Sonora.

The "dactyloides" leaf form is also found in Erigeron seemannii, E. inoptatus and E. coroniglandifer and I believe E. dactyloides is most closely
related to E. seemannii rather than E. oreophilus All three species have
a densely stipitate-glandular vestiture. Erigeron seemannii differs from E.
dactyloides in its cauline leaves with clasping to subclasping, ampliate bases
and its pappus without an outer series of scales. See further comments following E. seemannii.

Erigeron dactyloides and E. oreophilus have been collected in close proximity. Two of the collections cited above were of mixed species: Townsend & Barber 306 (CAS) and Mearns 2232 (DS) are typical E. oreophilus.

- Erigeron delphinifolius Willd., Enum. Hort. Berol. 2:873. 1809. Type: In America meridionali, Humboldt & Bonpland s.n. (holotype: B [not seen], drawing by Klatt in GH!). Diplopappus delphinifolius (Willd.) Cass., Dict. Sci. Nat. 25:96. 1822. Polyactis delphinifolius (Willd.) Cass., Dict. Sci. Nat. 37:485. 1825; 50:483. 1827. Polyactis delphinifolius (Willd.) Less., Syn. Comp. 189. 1832. Polyactidium delphinifolium (Willd.) DC., Prodr. 5:282. 1836. Erigeron delphinifolius subsp. delphinifolius Cronq., Brittonia 6:263. 1947.
- Achaetogeron fisheri Larsen, J. Washington Acad. Sci. 38:200. 1948. Type: MÉXICO, México: Amecameca, 9000 ft, 29 Jul 1924, G.L. Fisher s.n. (holotype: MO!; isotype: ARIZ!).
- Achaetogeron sophiifolius Larsen, J. Washington Acad. Sci. 38:200. 1948. Type: MÉXICO, Durango: City of Durango and vicinity, Apr-Nov 1896, E. Palmer 158 (holotype: MO!; isotypes: MEXU!,NY!,UC-2 sheets!,US!).

Annual herbs from a woody but slender taproot. Stems 1(-5) from the base, 20-70(-170) cm tall, with (1-)4-10 primary branches on the upper 1/2-2/3, these usually branched also, antrorsely appressed-strigose on the upper 1/4-3/4, spreading to retrorse below that, appressed from bottom to top, essentially eglandular. Leaves strigose, sometimes minutely granular-glandular; basal leaves obovate, coarsely serrate or crenate to pinnately lobed, attenuate to a petiole 1/2-2/3 as long as the leaf; cauline leaves pinnatified to bipinnatified with 2-5 pairs of narrowly lanceolate to oblanceolate lobes, 15-90 mm long, 3-50 mm wide, not clasping, the lower petiolate, sessile and reduced in size upwards. Heads 7-14 mm wide, (2-)6-35 in a loose, corymbose capitulescence, on relatively naked peduncles mostly 1-7 cm long; phyllaries

3.1-6.2 mm long, minutely granular-glandular. Ray flowers 110-240(-325) in 2-3 series, corollas white, 8.0-14.9 mm long. Disc corollas 2.2-3.1 mm long. Achenes 0.9-1.6 mm long, with 2, thick ribs; pappus of 6-10(-12) caducous bristles nearly as high as the disc corolla, with an outer corona or series of scales 0.1-0.2 mm high or sometimes lacking. Chromosome number, n=9, 18 pairs.

Western sierra in Durango, Nayarit, Zacatecas, Jalisco and Aguascalientes, eastward (primarily in the trans-volcanic range) through Michoacán, Guanajuato, San Luis Potosí, Querétaro, Hidalgo, México, Morelos, Tlaxcala and Puebla; common in a variety of open vegetation or disturbed sites, common along roadsides; mostly 1700-2750 m; Jul-Nov and sporadically throughout the year at lower elevations. Map 1.

Representative collections examined: MÉXICO, Aguascalientes: ca 20 km E of Rincon de Romos, 4-8 Sep 1967, McVaugh 23732 (DS, MICH). Distrito Federal: Santa Fe, 17 Aug 1865, Bourgeau 717 (GH). Durango: City of Durango and vicinity, Nov 1896, Palmer 928 (GH, MEXU, MO, NY, UC, US); Sandia Station, 16 Oct 1905, Pringle 13548 (CAS, GH, LL, MICH, US). Guanajuato: Ravin de Esperanza, Aug 1895, Duges s.n. (GH). Hidalgo: Buena Vista, near Sierra de Pachuca, 4 Aug 1904, Pringle 13452 (GH, MICH, US). Jalisco: Río Blanco, Jul 1886, Palmer 166 (GH, MICH, NY, PH, US). México: Flor de Maria, 21 Aug 1890, Pringle 3235 (GH, MICH, MO, MU, MEXU, NY, PH, UC, US). Michoacán: Tancitaro, 22 Oct 1940, Hinton 15556 (LL, MICH, NY, UC, US); ca 8 km S of Uruapán, 11-15 Oct 1961, King & Soderstrom 4773 (MEXU, MICH, NY, SMU, TEX, UC, US). Morelos: México to Cuernavaca toll road, 6 Jan 1957, Langman 4119 (PH). Nayarit: Arroyo Santa Rosa, W of Santa Teresa, 100 air km NNE of Tepic, 21-24 Oct 1979, Breedlove 44542 (CAS). Puebla: between Acatzingo and El Seco, 10 Oct 1944, Sharp 441262 (GH, MEXU, NY, TENN). Querétaro: 1.5 mi W of El Ciervo, 30 Aug 1965, Flyr 601 (SMU). San Luis Potosi: Region of San Luis Potosi, 1878, Parry & Palmer 389 (DS, MO, NY, PH, US). Tlaxcala: ca 3 mi N of Zacatelco on Hwy 119, 24 Jan 1960, King 2254 (MICH, TEX). Zacatecas: 13 mi ESE of Sombrerete on Hwy 45, 5 Aug 1977, Nesom 610 (NCU).

Erigeron delphinifolius has been considered conspecific with E. neomexicanus (Cronquist, 1947), but the latter is a perennial from a strongly woody base. Further, the two taxa are allopatric with distinct geographic ranges and occur in very different types of habitats.

In Durango the cauline leaves of Erigeron delphinifolius have a stronger tendency to be pinnatifid, the upper leaves are often more densely glandular and the appressed pubescence is more restricted to the upper portions of the stems than in plants to the southeast. The type of Achaetogeron sophiifolius has tripinnatifid leaves, but this apparently represents only an extreme of the tendency for greater lobing in Durango.

One collection from northeastern Durango (Pringle 13548) has an exceptionally high number of ray flowers (ca 350-400), extremely large and persistent basal leaves and only 2-4 pappus bristles per achene.

Erigeron delphinifolius is the only annual besides E. inoptatus and E. annuactis in sect. Polyactis, the only species with strong colonizing tendencies and the only species that ranges outside of the western Sierra Madre. The center of morphological variability for the species is in the westernmost part of its range, near the center of species diversity for the section and it is almost certain that the wide distribution of E. delphinifolius across the trans-volcanic mountains was attained after its evolutionary origin in the western sierra.

Erigeron eruptens Nesom, sp. nov. Type: MÉXICO, Chihuahua: Mpio. Ocampo, 18 mi SE of jct of Tomochic-Yepachic road on road to San Juanito, 2 mi SE of Yoquiva (ca 24 mi SE of Basaseachic), [ca 28° 07'N, 108° 02'W], on ca 45° NW-facing, open slope, ca 7500 ft, 27 Apr 1984, Spellenberg et al. 8070 (holotype: TEX!; isotypes: ARIZ,ASU,COLO!, ENCB,INIF,K,MEXU,NMC,NY,RSA,UC,UNM,US,UTEP).

Ex speciebus sectionis *Polyactis* habitu dense cespitoso, ramis caudicis ascendentibus, et caulibus strictis quasi scaposis, minute stipitati-glandulosis distinguenda.

Herbaceous perennials from a taproot or fibrous roots, usually densely cespitose (forming clumps up to 4 dm in diameter) from several, ascending caudex branches, each branch producing an obconic rosette of erect basal leaves and 1-numerous, erect, merely bracteate stems. Stems 7-32 cm tall, unbranched or rarely with a branch on the upper half, minutely but prominently stipitate-glandular, very sparsely hispid-pilose, the hairs sometimes slightly deflexed, ascending appressed in S Chihuahua. Basal leaves obovate in outline, pinnatifid with (1-)2-4 pairs of obovate lobes, these sometimes coarsely toothed, mostly 10-30 mm wide (lobe tip to tip) (-45 in S Chi), 2-12 cm long with a petiolar region ca half as long as the leaf, sparsely to densely strigose-hispid with arching hairs, eglandular or essentially so; cauline leaves all reduced to linear-lanceolate, non-clasping bracts. Heads solitary on essentially scapose stems, 8-15 mm wide; phyllaries 3.8-5.0 mm long, densely and minutely stipitate-glandular, otherwise sparsely pilose. Ray flowers 26-72 in 1 series, corollas white, drying white to light lavender, 8-11 mm long. Disc corollas 3.5-4.5 mm long. Achenes oblong, ca 1.0 mm (1.9 mm in S Chi) long, with 2(-3) thin ribs; pappus of 10-12 basally caducous bristles, with an outer series of setae and linear scales 0.1-0.2 mm high.

Southwestern to southern Chihuahua; open banks, usually steep and of loose and bare soil, or crevices or ledges of cliffs, in areas of pine or pine-oak forest, commonly with fir; 2150-2400 m; flowering April-June(-August). Map 5.

Additional collections examined: MÉXICO, Chihuahua: Mpio. Bocoyna: ca 15 air mi SW of San Juanito, 6.5 mi SE of jct of road to Maguarichi from San Juanito-Basaseachic road, 1 mi NW of Talayotes, in mesic, cool canyon bottom, area called "Arroyo del Gato" on banks, 28 Apr 1985 Spellenberg et al. 8114 (TEX - dups not seen at ID, MEXU, NMC, NY); 0.9 mi from jet of San Juanito-Basaseachic road on road to Maguarichi, along flowing stream, 19 May 1984, Ayers 393 (TEX); road to Mojarachi from the San Juanito-Creel road, moist areas of steep slopes, 18 May 1985, Grimes 2862 (CIIDIR, MEXU, RM, TEX, UC, UCR, WIS). Mpio. Ocampo, Cascada de Basaseachic, in large rocks at base of large boulders, near base of falls, 21 May 1984, Ayers 415 (TEX); Mpio. Guadalupe y Calvo, 81 km SW of El Vergél toward Guadalupe y Calvo, 3.2 km S of bridge in Turuachi, deep area of canyon, crevices and talus, 26 Aug 1983, past fir and frt, Nesom 4973 (MEXU, MICH, NMC, TEX); Mpio. San Pablo Balleza, 43.5 km SW of EL Vergél on road to Guadalupe y Calvo, N-facing side of deep canyon with pine-fir-oak, cliff crevices, loose talus below road, 26 Aug 1983, Nesom 4991 (ARIZ, ASU, CIIDIR, COLO, CAS, CHAPA, ENCB, F, GH, GUADA, K, MEXU, MICH, MO, NMC, NY, RM, RSA, UC, US); 22.0 mi SW of El Vergél, 0.1 mi N of Rio Verde bridge, N-facing cliff above road, area of pine-oak woods, 25 Aug 1984, Nesom 5167 (TEX).

The epithet is grammatically distorted in reference to the emergent-

appearing rosette of basal leaves.

Erigeron eruptens is recognized among the species of sect. Polyactis by its monocephalous, essentially scapose stems and large, densely cespitose, basal rosettes of erect-ascending, pinnatifid leaves produced from numerous, ascending caudex branches. The plants from southern Chihuahua apparently are disjunct from the more northern population system and tend to have larger leaves and heads as well as ascending-appressed pubescence and fewer glands on the stems and phyllaries, but in other characters they appear to represent the same species. In the Basaseachic area, E. eruptens is somewhat similar to E. basaseachensis in habit but differs from it in its generally larger size, lack of rhizomes, presence of glands, larger heads on scapose stems and longer disc corollas.

Erigeron griseus (Greenm.) Nesom, Sida 9:224. 1982. Based on Achaetogeron griseus Greenm., Proc. Amer. Acad. Arts 41:254. 1905. Type: MÉXICO, Durango: Vicinity of the city of Durango, Apr-Nov 1896, E. Palmer 821 (holotype: GH!; isotypes: UC!, US!).

Bellis garciae S.F. Blake, Contr. U.S. Natl. Herb. 22:593. 1924. Type: MÉXICO, Durango: State of Durango, 1000 m, P. Ibana Garcia 310. (holotype: US!). Achaetogeron garciae (S.F. Blake) Larsen, J. Washington Acad. Sci. 38:201. 1948.

Perennial herbs from fibrous roots, sometimes with short, fibrous-rooted

rhizomes, caudex simple or with several, short, ascending branches. Stems 11-36 cm tall, unbranched or sometimes with 1-4 branches on the lower half, moderately thin-strigose, less commonly spreading on the lower half or rarely from top to bottom, eglandular or very sparsely and inconspicuously granular-glandular. Basal leaves usually deciduous by flowering, 7-130 mm long, the blades obovate, attenuate to a petiole 1/2-2/3 as long as the leaf, with 1-4 pairs of serrate or crenate teeth or obovate to lanceolate lobes, less commonly entire, the cauline not clasping, becoming entire and sessile upwards, moderately strigose, mostly eglandular. Heads 7-17 mm wide, solitary, the peduncles 1-14 cm long, often noticeably dilated just under the heads; phyllaries 3.1-5.5 mm long, strigose to strigose-hirsute, minutely granularglandular, at least the inner with relatively broad, hyaline, often purplish margins. Ray flowers 40-230, the corollas white or violet, (3.0-)8.0-14.9 mm long. Disc corollas 2.0-3.5 mm long. Achenes 0.8-1.1 mm long, with 2-4 thick ribs, sparsely strigose; pappus a minute, cartilaginous crown less than 0.1 mm high, with a smooth, even apex, sometimes almost completely absent. Chromosome number, n=9 pairs.

Central to southern Durango and adjacent Nayarit; grassy or rocky sites in pine-oak to pine woodlands; 2250-2700 m; (Jun-)Jul-Oct. Map 7.

Representative collections examined: MÉXICO, Durango: Mpio. El Salto, 6 mi W of Las Adjuntas on Hwy 40, 19 Aug 1981, Nesom 4446 (ARIZ, ASU,CAS,COLO,ENCB,MEXU,MICH,NMC,NY,RM,TEX,UCR); Mpio. Durango, Otinapa, 25 Jul-5 Aug 1906, Palmer 426 (CM,DS,NY,UC,US). Nayarit: between Santa Gertrudio and Santa Teresa, 8 Aug 1897, Rose 2087 (US).

Erigeron griseus is similar and closely related to E. wislizeni. See comments under that species.

The ray color in *Erigeron griseus* is mostly white; strikingly different, violet-rayed forms are clustered mostly to the east of El Salto, but they are also scattered elsewhere. As in *E. wislizeni*, variation in other aspects of morphology is not correlated with ray color and the color forms are not given taxonomic recognition.

Nesom 4446 represents an unusually short-rayed and small-statured population of Erigeron griseus.

Erigeron griseus is superficially very similar to E. astranthioides De Jong & Nesom, which also grows along Highway 40 in Durango. Both taxa are essentially monocephalous and epappose, but the latter is related to the group of species that includes E. forreri (E. Greene) E. Greene and E. galeottii (A. Gray ex Hemsl.) E. Greene (De Jong & Nesom, 1982), rather than sect. Polyactis. Erigeron astranthioides differs from E. griseus in its thin, scale-leaved stolons (fragile and easily broken off during collecting), stems very sparsely spreading-pubescent, leaves with glabrous to glabrate lamina, the

basal sharply attenuate to a distinct petiole, the cauline sessile, subclasping, phyllaries thin-herbaceous from base to tip, obovate to oblong-obovate, ray corollas non-reflexing, collecting appendages of the style branches (disc flowers) lanceolate to narrowly triangular, 0.3-0.4 mm long and achenes glabrous with thin nerves.

Erigeron inoptatus A. Gray, Proc. Amer. Acad. Arts 21:387. 1886. Type: MÉXICO, Chihuahua: on riverbank in sand, 150 mi N of Batopilas, Aug-Nov 1885, E. Palmer 442 (holotype: GH!; isotype: US!).

Erigeron alcicornutus Greenm., Proc. Amer. Acad. Arts 41:255. 1905. Type: MÉXICO, Chihuahua: alluviums of Arroyo. Ancho, Sierra Madre, 15 Oct 1887, C.G. Pringle 1273 (holotype: GH!; isotypes: MEXU!, NY-2 sheets!, PH!, RSA!, US!).

Annual herbs from a slender taproot, single-stemmed from the base. Stems, leaves and phyllaries moderately to densely hirsute-pilose, densely stipitate-glandular. Stem 24-175 cm tall, with 1-8 branches on the upper half, usually with secondary branches. Basal leaves usually absent by flowering; cauline leaves numerous, the basal petiolate, sessile above with clasping, ampliate bases, the middle 2.5-8.5(-11) cm long, relatively unreduced in size upwards, 7-66 mm wide (lobe tip to tip) with a midregion of even width, margins with 1-5 pairs of lanceolate to obovate lobes, sometimes bipinnatifid, with sinuses extending 1/3-2/3 to the midvein. Heads in a loose corymbose capitulescence, 7-12 mm wide, on peduncles 4-90 mm long; phyllaries 3.5-5.5 mm long. Ray flowers 325-450 in 3-4 series, corollas white, 6.2-9.5 mm long, 0.2-0.5 mm wide, rarely very short or completely absent. Disc corollas 1.8-2.5 mm long. Achenes 0.8-1.0 mm long, with 2, thin ribs, glabrous; pappus of 0-4 very brittle, basally caducous bristles 1/3-1/2 the disc corolla height, the number of bristles variable among flowers of a single plant but usually constant within one head, with an outer, minute, cartilaginous rim. Chromosome number, n=9 pairs.

Central to southern Chihuahua and probably northern Durango; clearings, pastures, disturbed sites, streambeds, grasslands or areas of pine or pine-oak woods; 2150-2300 m; Aug-Oct. Map 6.

Representative collections examined: MÉXICO, Chihuahua: Mpio. San Pablo Balleza, town of El Vergél, ca 80 mi S of Parral on Hwy 24, 21 Oct 1986, Nesom 5762 (MEXU,NMC,NY,TEX); Mpio. Guerrero, ca 28 mi SSW of La Junta on road to San Juanito, 18 mi S of jct with road to Tomochic, 24 Aug 1981, Nesom 4489 (ARIZ,ASU,CAS,COLO,ENCB,F,MEXU, MICH,MO,NMC,NY,RM,TEX,US); [Mpio. Guerrero], "Barranca Colorad," Sierra Gazachic, 35 km SW of Miñaca, 16-17 Sep 1934, Pennell 18925 (GH, NY,PH,US).

Erigeron inoptatus is distinctive in its annual, single-stemmed habit, densely stipitate-glandular herbage, narrowly oblong, clasping cauline leaves, nu-

merous ray flowers with very narrow ligules, glabrous, thin-ribbed achenes and reduced pappus. The plants of the type collection are somewhat atypical. On the holotype, there is only a single series of ray flowers and these have such short ligules that Gray assigned E. inoptatus to sect. Coenotus, which at the time, contained species that have since been transferred to Conyza. Ray flowers are completely lacking on the isotype.

The vestiture and leaf shape and base of *Erigeron inoptatus* suggest that it is most closely related to *E. seemannii*.

Erigeron nacoriensis Nesom, sp. nov. Type: MÉXICO, Sonora: Nacori, [29° 04'N, 110° 03'W], 3750 ft, 1 Dec 1890, C.V. Hartman 271 (holotype: GH!).

E. eruptentem Nesom similis sed caulibus eglandulosis manifeste foliatis, capitulis minoribus, phyllariis eglandulosis, corollis radii et disci multo brevioribus differt.

Perennial herbs from fibrous roots, producing a system of woody, ascending, distally thickened, caudex branches, each with a rosette of leaves. Stems ascending-erect, 14-22 cm tall, unbranched or with 1-2 branches above the middle, moderately pubescent with appressed to closely ascending trichomes 0.2-0.6 mm long, eglandular. Leaves moderately strigose, minutely but prominently granular-glandular; basal leaves 25-45 mm long, the blade obovate with a rounded, mucronulate apex, pinnately divided with 2-4 pairs of obovate lobes, 10-22 mm wide, sharply tapered to a petiole 5-20 mm long; cauline leaves 10-26 mm long, elliptic-oblanceolate, 2-10 mm wide, entire or with 1-3 shallow teeth, sessile or the lower with a petiole 1-3 mm long, not clasping, relatively even-sized up to the capitulescence, where reduced to tiny bracts. Heads 5-7 mm wide, solitary on peduncles 35-55 mm long; phyllaries sparsely strigose, eglandular, in 2-3 subequal series, with broad, thickened, lateral zones and narrow, scarious and sometimes slightly lacerate margins, basally fused into a ring of tissue, 2.5 mm long, the outermost 1/3-1/2 as long as the inner. Ray flowers ca 60-80 in 1 series, the corollas white, drying white to light lavender, 4.8-6.0 mm long. Disc corollas 2.4-3.0 mm long. Achenes 0.9-1.0 mm long, with 2, very thin ribs; pappus of 10-14 bristles with an outer series of setae 0.1-0.2 mm high.

Known only from the type collection. Map 5.

Erigeron nacoriensis is similar to E. eruptens in its habit of ascending caudex branches with basal rosettes and mostly simple stems with solitary heads and its relatively few ray flowers and pappus of bristles. It differs from E. eruptens in its prominently leafy, eglandular stems, smaller heads with eglandular phyllaries and much shorter ray and disc corollas. Further, in the southern part of the range of E. eruptens, the plants have appressed-strigose stem pubescence, but in west-central Chihuahua, where the range of E. eruptens is closest to Nacori, the stems are hispid-pilose. The collection

of E. nacoriensis was made ca 200 km NW of the nearest collection of E. eruptens. The collection was probably made in the Sierra Nacori, just east of the town of Nacori. According to Marshall (1957), a deciduous oak woodland would be found there at the elevation noted in the collection data. Other collections made by Hartman (25 Nov 1890, 274-GH; 2 Dec 1890, 285-GH,US), also labelled "Nacori," were of E. neomexicanus, a species typically found in oak to pine woodlands.

Erigeron neomezicanus A. Gray, Proc. Amer. Acad. Arts 19:2. 1883. Type: UNITED STATES, New Mexico: Grant Co., mountains of the Copper Mines, 1851, C. Wright 1170 (lectotype designated here: GH!; isolectotypes: GH-2 sheets!, NY!, US!). E. delphinifolius Willd. subsp. neomezicanus (A. Gray) Cronq., Brittonia 6:263. 1947.

Among the syntypes cited by Gray ("Wright, Bigelow, Thurber, Palmer, Lemmon"), the Wright ones are distributed to various herbaria. The lectotype is among the three sheets at GH originally annotated by Gray as *E. neomexicanus*.

Perennial herbs from strongly woody bases and roots. Stems 15-65 cm tall, with 1-15 primary branches on the upper 1/2-1/3 of the stem, sometimes with secondary and tertiary branches, moderately to densely strigose with appressed to ascending trichomes, sometimes spreading at the base or over the whole stem, eglandular or rarely minutely granular-glandular. Leaves strigose, sometimes minutely glandular, the basal entire to toothed or pinnatifid, usually absent at flowering, the cauline 11-55 mm long, the lower attenuate to a petiole 1/4-1/2 as long as the leaf, not clasping, deeply pinnatifid with 2-4(-5) pairs of lobes or sometimes slightly bipinnatifid, leaf shape often highly variable within populations, 6-35 mm wide, gradually or barely reduced in size upwards until the peduncles. Heads 7-12 mm wide, on peduncles 3-55 mm long, in a loose, corymbose capitulescence; phyllaries 3.6-4.9 mm long with the outermost 1/3-2/3 as long, strigose to hirsute, the trichomes mostly arising from the midregion, eglandular or sometimes minutely glandular. Ray flowers 70-150 in 1-2 series, corollas white, (2-)6-15 mm long. Disc corollas 2.5-3.3 mm long, often noticeably inflated and indurated above the constricted lower part. Achenes 1.0-1.3 mm long, with 2, relatively thin, lateral ribs, commonly with 1-2 very thin ribs on the flattened faces, sparsely strigose; pappus of (8-)10-12 bristles, with an outer series of setae 0.1-0.2 mm high. Chromosome number, n=9, 18 pairs.

Arizona, New Mexico, Sonora and northwestern Chihuahua, rare to southern Chihuahua; open, rocky sites, from grasslands into oak or pine woodlands, often with madroño, juniper, or fir; 1100-2700(-3000) m; (Jul-)Aug-Oct (Dec). Map 3.

Representative collections examined: MÉXICO, Chihuahua: Guasaremos, Rio Mayo, 16 Sep 1935, Gentry 1828 (GH); Mpio. Guadalupe y Calvo,

summit of Cerro Mohinora, ca 13 mi SW of Guadalupe y Calvo, 27 Aug 1987, McDonald & Martinez 2372 (MEXU,TEX,XAL); Mpio. Ocampo, along trail to bottom of Cascada de Basaseachic, Nesom 5559 (TEX). Sonora: Sierra de los Ajos, 29 Jul 1952, Marshall 87 (ARIZ,CA,UC).

UNITED STATES, Arizona: Cochise Co.: Chiricahua Mts.: ca 4 mi W of Biological Station, just E of E Turkey Creek, 27 Aug 1981, Nesom 4512b (NY,TEX); 8 mi W of Biological Station, 27 Aug 1981, Nesom 4514 (CAS, CIIDIR,CHAPA,DAV,NCU,NMC,OBI,RM,RSA,TEX,UCR). New Mexico: Grant Co.: 3 mi N of Pinos Altos on Hwy 25, 17 Sep 1967, Hess 1497 (ARIZ,NCU).

In the Atascosa Mountains of southwestern Santa Cruz County, Arizona, Erigeron neomezicanus commonly has ligules much shorter (2-6 mm long) than typical for the species (6-15 mm long).

See the comments following Erigeron delphinifolius for observations on the differences between it and E. neomexicanus.

Cronquist (1947) treated Erigeron neomexicanus and E. oreophilus as conspecific, and in most characters they are virtually identical. Erigeron neomexicanus tends to have slightly shorter phyllaries and the achenes often have nerves on the flattened faces. The differences between them in pubescence, however, are consistent and conspicuous and appear to be more complex than if only a single species were involved (see key and comments below).

In contrast to their extensive area of sympatry, E. neomexicanus is rare in southwestern New Mexico and eastern Chihuahua, where E. oreophilus is abundant; but from northeastern Sonora, where E. neomexicanus is abundant, there have been almost no collections of E. oreophilus. In Arizona, both taxa occur in some mountain ranges (e.g., the Chiricahua, Huachuca, Santa Rita and Santa Catalina mountains), but in other ranges only one or the other is known (e.g., E. neomexicanus in the Patagonia, Atascosa and Sierra Ancha mountains; E. oreophilus in the Rincon, Baboquivari, Mazatzal and Pinaleño mountains, including Mt. Graham). In the area of Basaseachic, Chihuahua, E. neomexicanus is very rare; E. oreophilus is common. And E. oreophilus extends much further south than E. neomexicanus.

The following couplet contrasts the two taxa. Illustrations of Type A, B and C trichomes are found in Nesom (1976).

Stems, leaves and phyllaries with Type A trichomes usually absent to very sparse, spreading, 0.6-2.0 mm long, averaging 1.0 mm, Type B trichomes absent or rare, Type C (glandular) trichomes usually dense, large (50 - 200µm high), capitate and conspicuous .... E. oreophilus

Stems, leaves and phyllaries moderately to densely pubescent with appressed to spreading Type A trichomes 0.1-0.8(-2.0) mm long, averaging 0.4 mm, Type B trichomes abundant and prominent, Type C (glandular)

trichomes usually absent, minute  $(30 - 70\mu m \text{ high})$  and non-capitate when present ...... E. neomexicanus

In areas where Erigeron neomexicanus and E. oreophilus occur in close proximity, there is little infra-populational variation in pubescence and plants that might be considered of intermediate morphology may be present but they are not abundant, despite Cronquist's assertion that "E. oreophilus grades directly into E. neomexicanus." In the Chiricahua Mountains of Arizona I have observed several populations of both taxa growing in close proximity (e.g., Nesom 4512a and 4512b) with little or no evidence of hybridization. Plants that I have identified as E. neomexicanus are much more variable both in leaf morphology and vestiture than E. oreophilus, and most putative hybrids are usually more similar to E. neomexicanus - they have relatively dense, spreading or appressed Type A trichomes and sparse, mostly minute Type C trichomes on the phyllaries and sometimes on the uppermost leaves and stems. One intermediate individual, for example, from the Chiricahua Mountains (Roth s.n.-TEX) is stipitate-glandular and has sparse, appressed, Type C hairs.

Regional floras (Kearney & Peebles, 1951; Lehr, 1978; McDougall, 1973; Martin & Hutchins, 1980) have maintained the two as separate species. The unusually close correspondence of their overall geographic ranges, however, and their morphological similarity lend credence to Cronquist's hypothesis that they are conspecific. If Cronquist is correct, the large area of sympatric geographic distribution of the two forms implies that some form of complex dimorphism or polymorphism may exist. But my own experience leads me to the conclusion, albeit tentative, that there are two species, which may hybridize, but not so frequently that the morphological boundary between the taxa is extensively blurred.

Erigeron oreophilus Greenm., Proc. Amer. Acad. Arts 41:257. 1905. Type: MÉXICO, Chihuahua: Norogachi, southern part of the state, 8500 ft, Nov 1885, E. Palmer 419 (lectotype [designated here]: GH!; isolectotypes: MEXU!, PH!, US-2 sheets!). E. delphinifolius Willd. subsp. neomexicanus (A. Gray) Cronq. var. oreophilus (Greenm.) Cronq., Brittonia 6:264. 1947.

Erigeron oreophilus Greenm. forma tenuilobus Greenm., Proc. Amer. Acad. Arts 41:258. 1905. Type: MÉXICO, Sinaloa: Sierra de Choix, 15 Oct 1898, E.A. Goldman 255 (holotype: GH!; isotype: US!).

Erigeron oreophilus Greenm. forma latilobus Greenm., Proc. Amer. Acad. Arts 41:258. 1905. Type: MÉXICO, Chihuahua: base of Mt. Mohinora, 12.8 km from Guadalupe y Calvo, 7000-7500 ft, 23-31 Aug 1898, E.W. Nelson 4861 (holotype: GH!; isotype: US!).

Achaetogeron pringlei E. Larsen, J. Washington Acad. Sci. 38:200. 1948.

Type: MÉXICO, Chihuahua: cool slopes, Sierra Madre, 10 Oct 1888, C.G. Pringle 1625 (holotype: MO!; isotype: UC!).

Perennial herbs from strongly woody bases and roots. Stems 25-90 cm tall, with 2-20 primary branches on the upper 1/2-1/3 of the stem, sometimes with secondary and tertiary branches, sparsely hispid-pilose with long trichomes, prominently stipitate-glandular on at least the peduncles or upper portions of the stems. Leaves sparsely hispid-pilose, densely stipitateglandular on at least the upper, the basal entire to toothed or pinnatifid, usually absent at flowering, the cauline 13-55 mm long, the lower attenuate to a petiole 1/4-1/2 as long as the leaf, not clasping, deeply pinnatifid with 2-4(-5) pairs of lobes or sometimes slightly bipinnatifid, 6-35 mm wide, gradually or barely reduced in size upwards until the peduncles, rarely the upper coarsely toothed to entire, the blades then obovate. Heads 8-12 mm wide, on peduncles 4-45 mm long, in a loose, corymbose capitulescence; phyllaries 4.5-5.5 mm long with the outermost 1/3-3/4 as long, densely stipitate-glandular, otherwise glabrous or very sparsely hispid-pilose. Ray flowers 75-130 in 1-2 series, corollas white, 8-14 mm long. Disc corollas 2.8-3.5 mm long, often noticeably inflated and indurated above the constricted lower part. Achenes 1.0-1.2 mm long, with 2, relatively thin, lateral ribs, sparsely strigose; pappus of (8-)10-12 bristles, with an outer series of setae less than 0.1 mm high. Chromosome number, n=9 pairs.

Arizona, New Mexico, Sonora through Chihuahua, rare southward to southeastern Durango; open, rocky habitats, often cliff ledges or crevices, in oak to pine woodlands; 1250-2800(-3000) m; (May-)Jul-Oct(-Dec). Map 4.

Representative collections examined: MÉXICO, Chihuahua: Río Mayo, 19 Sep 1936, Gentry 2799 (ARIZ,GH,MO); 6.5 mi SW of El Vergél on road to Guadalupe y Calvo, 27 Aug 1983, Nesom 4936 (TEX); La Bufa Mt. above Cusihuiriachic, 31 Aug 1887, Pringle 1271 (GH,MEXU,MICH,MO,PH,US); Mpio. Bocoyna, slopes of Río Oteros W of Creel, 16 Oct 1977, Bye & Weber 8238 (LL). Durango: ca 20 air km WNW of Santiago Papasquiaro, 9 Jul 1983, Worthington 10926 (TEX,UTEP); ca 50 mi NW of Santiago Papasquiaro, 19 Sep 1982, Spellenberg & Zimmerman 6768 (TEX); Mpio. Suchil, Rancho Temascal, arroyo Los Indios, 14 Oct 1985, Alvarado 321 (TEX). Sonora: Dist. Alamos, Arroyo Agua Blanco, 11 Oct 1933, Gentry 512 (ARIZ,DS,MICH); Cañon Internacional, 23 Aug 1940, White 3507 (MEXU,MICH).

UNITED STATES, Arizona: Cochise Co., ca 4 mi W of Biological Station, just E of E Turkey Creek, 27 Aug 1981, Nesom 4512a (NY,RM,TEX); Graham Co., Pinaleño Mts., near entrance to Shannon CG and Heliograph Peak Road, 29 Aug 1981, Nesom 4530 (ARIZ,COLO,MO,NY,TEX). New Mexico: Catron Co., Hillsboro Peak, 19 Jul 1904, Metcalfe 654 (ARIZ,NMC,US).

I recognize Erigeron oreophilus var. dactyloides Greenm. as a distinct

species of sect. *Polyactis*, more closely related to *E. seemannii* than to *E. oreophilus*.

Plants from one locality in the Rio Mayo region of Chihuahua (Gentry 2799) are the most variable of any single collection of Erigeron oreophilus studied. At least three distinctive morphotypes were present at this locality, only one of which (ARIZ,MO) is typical of plants found over the rest of the range. Two of the morphotypes have appressed Type A pubescence on the upper stems. One of these has a cespitose habit, producing up to 8 decumbent or ascending, caudex-like branches from the base. These cespitose plants (GH,MO) have densely glandular phyllaries but only Type B trichomes on the peduncles. The other atypical morph (ARIZ,GH,MO) has a typical habit but has conspicuous Type C glands mixed with appressed Type A trichomes on the peduncles. All three forms are apparently diploid, judging from the even-sized and highly stainable pollen, but the origin of the two atypical forms is unknown. Other collections of E. oreophilus from the Rio Mayo region (e.g., Gentry 2805-ARIZ) have been of typical plants. Typical Erigeron neomexicanus also occurs in the Rio Mayo region (Gentry 1828).

Erigeron oreophilus is known from only few collections in Durango, where the plants have very small glands.

Erigeron podophyllus Nesom, sp. nov. Type: MÉXICO, Chihuahua: Mpio. Ocampo, ca 16 km (air) ENE of Ocampo, ca 2.5 km S of village of Basasaeachic, base of Cascada de Basaseachic, 28° 02'N, 107° 55'W, barranca at base of falls of Río Candameña, 17-20 Oct 1986, G. Nesom 5596 with L. Vorobik (holotype: TEX!; isotypes: ARIZ!,GH!,MEXU!, MO!,NY!,US).

Ex speciebus sectionis *Polyactis* rhizomatibus longis crassis, caulibus brevibus pauci-ramosis, foliis confertis in caulibus, obovaticuneatis dentatis in extremis distalibus, capitulis solitariis, et setis pappo numerosioribus distinguenda.

Perennial herbs from long, remotely branched rhizomes, forming dense, clonal populations. Stems 10-22 cm tall, quickly ascending at the rhizome tips, sometimes minutely granular-glandular, moderately to densely but weakly hispid with coarse to thin, white to translucent hairs, noticeably deflexed on the lower portions, antrorsely appressed to ascending on upper peduncles. Leaves sometimes clustered at rhizome tips but without a basal rosette, sparsely strigose-hispidulous on both surfaces, the lower cauline oblong- to obovate-cuneate to widely obovate, sometimes basally attenuate to a short, petiole-like base, not clasping, with 1-3(-4) pairs of coarse teeth or shallow lobes on the distal third, 7-18 mm wide, 10-35 mm long, gradually reduced in size upwards. Heads 9-12 mm wide, solitary on naked peduncles 2-6 cm long; phyllaries 4-6 mm long, stipitate-glandular, otherwise the outer sparsely

hispid. Ray flowers (50-)85-120 in 1-2 series, corollas white, drying white, 8-11 mm long. Disc corollas 2.5-4.0 mm long. Achenes ca 0.8 mm long, with 2 orange ribs, sparsely strigose; pappus of 11-17 basally caducous bristles, slightly shorter than the disc corollas, with an outer series of linear scales 0.1-0.4 mm high.

Southwestern Chihuahua, endemic to the deep barranca at the base of La Cascada de Basaseachic, ca 1000 m below the top of the falls in the open, treeless area mostly in the spray zone, this dominated by E. podophyllus and Aegopogon with other forbs; 1750-1800 m; flowering (Mar-)April-May and again in October. Map 5.

Additional collections examined: MÉXICO, Chihuahua: [Type locality]: 30 Mar 1975, McLaughlin 556 (ARIZ); 19 Aug 1984, Nesom 5107 with Lewissterile but showing developing rhizomes (ARIZ, ASU, COLO, NMC, MEXU, MO, NY, RM, RSA, TEX, US); 27 Apr 1986, Nesom 5438 with Spellenberg et al. (F, TEX, RM, MO); 14 Oct 1984, R. & M. Spellenberg 7940 (TEX, duplicates not seen at ASU, COLO, MEXU, NMC, NY, ID, RSA, UTEP).

Erigeron podophyllus is distinctive among all its relatives in sect. Polyactis in its long, thick rhizomes, short- and single-stemmed habit, obovate-cuneate, non-clasping leaves with a few, distal teeth or lobes and solitary heads. Also, the large number of pappus bristles is unique in the section and remarkable since E. podophyllus is probably the most narrowly restricted endemic and has the most strictly imposed external barriers to dispersal of any species in sect. Polyactis.

Erigeron polycephalus (Larsen) Nesom, Sida 9:224. 1982. Based on Achaetogeron polycephalus Larsen, J. Washington Acad. Sci. 38:200. 1948. Type: MÉXICO, Durango: San Ramón, 21 Apr-18 May 1906, E. Palmer 52 (holotype: MO!; isotypes: CM!, UC!, US!).

Achaetogeron corymbosus Larsen, J. Washington Acad. Sci. 38:201. 1948. Type: MÉXICO, Jalisco: canyons, moist rocks, Tuxpan, Feb 1904, C.A. Purpus 527 (holotype: GH!).

Suffrutescent, perennial herbs 1.0-1.5(-2.4) m tall, from woody roots. Stems usually with 3-12 primary branches on the upper half, these often with secondary and tertiary branches, appressed-pubescent or sometimes spreading, eglandular or rarely slightly stipitate-glandular. Cauline leaves sparsely to densely strigose, sometimes minutely glandular, lower margins sometimes long-ciliate, often tardily deciduous and deflexed on the lower stems, (3-)8-90 mm long, the blades 2-35 mm wide, elliptic to elliptic-oblanceolate, attenuate to a petiole 1/4-1/2 as long as the blade, margins serrate or crenate with 4-11 pairs of mucronulate teeth, rarely reduced to mucros, rarely with narrow, pinnate lobes. Heads 9-15 mm wide, 3-13 in a loose, bracteate corymb, on peduncles 4-30 mm long; phyllaries 3-7 mm long, sparsely to moderately hirsute-pilose, usually viscid-glandular. Ray flowers 60-110 in

1-2 series, corollas white, 6.5-15.0 mm long. Disc corollas 2.0-4.0 mm long. Achenes 0.9-1.0 mm long, with 2, thick ribs; pappus of 8-11 caducous bristles, with an outer, fimbriolate rib less than 0.1 mm high.

Western slope of the sierra in Durango, Sinaloa and Jalisco, mountains of Colima, Michoacán and Guerrero, but apparently not on the Pacific slopes of the latter two; steep habitats, commonly very moist, on mountainsides, cliffs, tropical deciduous forest, oak-palm, oak, pine with a mixture of hardwoods, to pine-fir or fir forests; 450-2850 m; (Nov-)Jan-Apr(-Aug). Map 2.

Representative collections examined: MÉXICO, Colima: brecha, El Zapote, out of Hacienda San Antonio, 27 Mar 1966, de Puga 215 (ENCB). Durango: 3-15 km toward El Salto from the Sinaloa boundary at El Palmito on Hwy 40, 13 Apr 1965, McVaugh 23612 (CAS,DUKE,LL,MICH,MO,NY,US). Guerrero: Mina, Aguazarca Filo, 21 Dec 1937, Hinton et al. 11314 (GH,MICH,NY,UC,US). Jalisco: ca 15 mi SE of Autlán, 13 Apr 1949, McVaugh 10279 (DS,DUKE,LL,MEXU,MICH,NY,US). Michoacán: near Uruapán, 21 Jan 1926, Woronow 2916 (US). Sinaloa: Sierra de Surotato, Canyon de Tarahumare, 17-24 Mar 1945, Gentry 7174 (GH,NY,MICH,PH,US).

Erigeron polycephalus is distinguished by its shrubby habit, corymbose, small-bracteate capitulescence, serrate or crenate leaves with elliptic or elliptic-oblanceolate blades and densely glandular phyllaries. It is a distinctive species but highly variable in the orientation and density of its pubescence.

Erigeron rhizomactis Nesom, sp. nov. Type: MÉXICO, Chihuahua: Mpio. Guadalupe y Calvo, N side of Cerro Mohinora, ca 13 mi SW of Guadalupe y Calvo, 25° 57'N, 107° 03'W; open, pine-fir woods with scattered spruce, 2950 m, 20 Aug 1988, G. Nesom 6449 with A. McDonald (holotype: TEX!; isotypes: ARIZ!, CAS!, COLO!, GH!, MEXU!, NY).

E. wislizeni (A. Gray) E. Greene similis et arcte affinis pedunculis longis pubescentia appressa caulium superarum et pappo coroniformi sed rhizomatibus valde tenuibus squami-foliiferis et foliis amplectentibus differt.

Herbaceous perennials with a thickened caudex, producing thin rhizomes up to 15 cm long. Stems 15-40 cm tall, usually simple, sometimes with 1-2 branches from about the middle or below, moderately strigose-sericeous, densely so under the heads, spreading to deflexed or retrorse near the base, eglandular. Leaves moderately long-strigose, eglandular, the basal absent at flowering but present at rhizome tips, mostly 2-9 cm long, the blades obovate, attenuate to a petiole ca half the leaf length; cauline leaves oblong-lanceolate to oblanceolate, sometimes narrowly so, entire or with 1-3 pairs of teeth on the upper third, mostly 2-10 mm wide, 30-65 mm long, clasping, relatively even-sized upwards. Heads 11-14 mm wide, solitary on naked peduncles 3-15 cm long; phyllaries 5-7 mm long, moderately hirsute-pilose, densely minutely

stipitate-glandular, at least on the distal half. Ray flowers 112-180 in 1-2(-3) series, corollas white, 11-16 mm long. Disc corollas 2.8-3.2 mm long. Achenes oblong, mature size not observed, sparsely strigose, 2-ribbed; pappus a hyaline corona of fused scales 0.1-0.2 mm high, without bristles.

Known only from the area around Guadalupe y Calvo in southern Chihuahua; pine-oak to pine-fir woods, margins, clearings, or in open woods, usually in relatively deep and loose soil; 2450-3000 m; Aug-Oct. Map 7.

Additional collections examined: MÉXICO, Chihuahua: Mpio. Guadalupe y Calvo: [Type locality, near the peak], 27 Aug 1987, McDonald & Martinez 2340 (MEXU,NMC,TEX,XAL); ca 13 mi E of Guadalupe y Calvo, 4.5 mi W of jct to Atascaderos, clearing in pine-oak woods, 2700 m, 24 Aug 1984, Nesom 5147a (MEXU,TEX,US); ca 11 mi E of Guadalupe y Calvo, 7.0 mi W of jct to Atascaderos, at woods edge in area of pine-oak, 2590 m, 24 Aug 1984, Nesom 5151 (MEXU,TEX); 10.9 mi W of jct to Atascaderos, ca 7 mi NE of Guadalupe y Calvo, area of fir with pine on surrounding hills, roadbank, 2780 m, 24 Aug 1984, Nesom 5155 (ARIZ,MEXU,NY,TEX,US); ca 12.5 mi SW of Guadalupe y Calvo on NW side of Cerro Mohinora, past turnoff to peak, downslope on road to Sinaloa, roadbank in oak-pine woods with fir and madroño, 2470 m, 22 Aug 1988, Nesom 6488 (MEXU,MO,NY,TEX).

Erigeron rhizomactis is very similar to E. wislizeni (A. Gray) Greene in its long peduncles, appressed upper stem pubescence and coroniform pappus, but it differs in its clasping leaves and very slender, scale-leaved rhizomes. The rhizomes are fragile and easily disconnected, but if carefully done, unearthing these plants reveals extensive interconnections among individuals of a colony. In my estimation, E. rhizomactis has probably been derived from the E. wislizeni complex as a high-elevation isolate.

Erigeron seemannii (Schultz-Bip. ex Seem.) E. Greene, Pittonia 2:168.

1891. Based on Polyactidium seemannii Schultz-Bip. ex Seem., Bot.
Voy. Herald 301. 1856. Type: MÉXICO, Durango: Sierra Madre,
NW of México, Nov-Jan 1849-50, Seemann 2026 (holotype: K!, MICHphoto!; isotype: GH!). Boltonia seemannii (Schultz-Bip. ex Seem.)
Benth. & Hook., Gen. Plant. 2:269. 1873. Achaetogeron seemannii
(Schultz-Bip. ex Seem.) A. Gray ex Hemsl., Biol. Centr. Amer. 2:120.
1881.

Perennial herbs, fibrous-rooted, from a short, thick, erect caudex or very short rhizome; stems, leaves and phyllaries sparsely to densely hirsute-pilose, stipitate-glandular with trichomes 0.1-0.4 mm high. Stems 15-70 cm tall, simple or usually with 1-6 branches on the upper 1/2-2/3. Basal leaves usually deciduous by flowering, the cauline oblong-lanceolate to oblanceolate, the largest 24-90 mm long, 8-37 mm wide, 2-3 times longer than wide, little or very gradually reduced in size upwards until near the capitulescence, mostly sessile with clasping to subclasping, slightly ampliate bases, margins with 1-

5 pairs of lanceolate, oblanceolate, or obovate lobes, sometimes bipinnatifid, the sinuses extending from the edge 1/3-2/3 to the midvein, the blade midregion usually of even width. Heads 10-15 mm wide, in loose corymbose capitulescence, on naked peduncles (0.5-)2.0-10.5 cm long; phyllaries 5.1-7.6 mm long, glandular, otherwise sparsely hispid-pilose or lacking hairs. Ray flowers 180-230 in 2-3 series, corollas white, 8.0-10.8 mm long. Disc corollas 2.3-3.2 mm long. Achenes 1.0-1.3 mm long, with 2, thick, whitish ribs, sparsely strigose; pappus of (1-6-)10-12 thick, caducous bristles ca 1/2-4/5 the disc corolla height, or rarely the disc or disc and ray achenes without bristles. Chromosome number, n=9 pairs.

Central Durango to southern Chihuahua; rocky soil, talus slopes, in areas of oak, pine, or pine-oak woods; 2150-2800 m; Aug-Oct(-Nov). Map 6.

Representative collections examined: MÉXICO, Chihuahua: Mpio. San Pablo Balleza, 12 mi NE of El Vergél on Hwy 24 from Parral, 21 Aug 1981, Nesom 4466 (ARIZ,CAS,CHAPA,COLO,DAV,ENCB,F,GH,GUADA,K,M,MEXU,MICH,MO,NMC,NY,OBI,OS,RM,TEX,UCR,UC,US,WAT,WIS). Durango: Mpio. Durango, ca 50 mi W of Durango and 15 mi NW of Los Coyotes RR station, Río Jarrál canyon, 30 Sep 1962, Cronquist 9571 (GH,MEXU, MICH,MSC,NY,TEX,US); Mpio. Durango, 6 mi W of Las Adjuntas on Hwy 40, 19 Aug 1981, Nesom 4445 (ARIZ,CAS,IBUG,MEXU,MO,NMC,NY,RSA, TEX).

Erigeron seemannii is recognized by its perennial habit, prominently stipitate glandular stems, leaves and phyllaries, stems with spreading pubescence from base to tip, relatively large, clasping, lobed, oblong-lanceolate to oblance-olate cauline leaves with broad midregions of even width, heads on long, naked peduncles and thick-ribbed achenes with extremely brittle pappus bristles that break off at the base at the slightest touch. The pappus is without an outer series, although the minute stubs of the broken-off bristles may falsely appear to represent one. In open habitats, the plants tend to be sprawling (vs. erect), the heads and leaves smaller, the pubescence denser and the glands smaller.

There appear to be two, widely separated population systems of *Erigeron seemannii*. Erigeron dactyloides, the species mostly closely related to E. seemannii, occurs as a third, equally separated population system still further north in Chihuahua (Map 6).

Erigeron subacaulis (McVaugh) Nesom, Sida 9:225. 1982. Based on Achaetogeron subacaulis McVaugh, Contr. Univ. Mich. Herb. 9:361. 1972. Type: MÉXICO, Aguascalientes: Sierra del Laurel, near the Jalisco border, ca 15-16 km SE of Calvillo, above Rancho de los Adobes, oak forest, 2500-2700 m, 26-28 Aug 1960, R. McVaugh 18434 (holotype: MICH!; isotypes: DUKE!, ENCB!, LL!, MICH!, NY!, US!).

Perennial herbs from fibrous roots, caudex simple or with a few, short

branches. Stems 7-40 cm tall, simple or with 1-3 branches on the lower 1/4-1/2, sparsely to moderately strigose with closely appressed hairs, sometimes ascending or spreading near the base, eglandular. Leaves sparsely archingstrigose, eglandular; basal leaves 2-10 cm long, 4-20 mm wide, petiolate, the blades oblanceolate to obovate, with 1-3 pairs of teeth or lobes, occasionally entire; cauline reduced upwards, lanceolate to oblanceolate, entire, sessile and non-clasping. Heads 8-12 mm wide, solitary on naked peduncles (1-)3-10 cm long; phyllaries all with prominently scarious margins, the outer 4.5-6.0 mm long, moderately hirsute-pilose, minutely punctate-glandular. Ray flowers 50-130 in 1-2 series, the corollas 7.0-8.5 mm long, apparently not reflexing with maturity. Disc corollas 2.2-2.9 mm long. Achenes ca 1.0-1.3 mm long, with 2, thick ribs, sparsely pubescent; pappus of 10-13 basally caducous bristles 0.7-2.5 mm long, 1/3-2/5 the disc corolla height, with an outer, blunt or barely fimbriate ring, less than 0.05 mm high.

Northern Jalisco and adjacent Zacatecas; areas of shrubby oaks or pine-oak woods; 2100-2500 m; Aug-Sep. Map 1.

Additional collections examined: MÉXICO, Jalisco: [topotype], Sierra del Laurel, near Calvillo, shrubby oaks, 2500 m, 27 Aug 1960, Rzedowski 14105 (ENCB). Zacatecas: Jalpa-Tlaltenango road, woods of Pinus and Quercus, humid and shady arroyo, 2100 m, 2 Aug 1971, Diaz Luna 2353 (ENCB, MICH).

Erigeron subacaulis is recognized by its stems simple or few-branched on the lower half, leaves entire to few-toothed and non-clasping, stem pubescence appressed-strigose and eglandular, heads on long, naked peduncles, outer and inner phyllaries with scarious margins and pappus of short bristles. On the few plants I have studied, the ray corollas do not appear to reflex at maturity, an anomalous feature within sect. Polyactis, but in other characters, the species clearly belongs there. In habit, E. subacaulis is most similar to E. griseus, but the latter lacks pappus bristles altogether. Erigeron subacaulis appears to be somewhat isolated from the other species of sect. Polyactis, both morphologically and geographically.

Erigeron wislizeni (A. Gray) E. Greene, Pittonia 2:168. 1891. Based on Achaetogeron wislizeni A. Gray, Mem. Amer. Acad. Arts 4:72. 1849. Type: MÉXICO, Chihuahua: llanos, Sierra Madre W of Chihuahua, Wislizenus s.n. (holotype: GH!).

Achaetogeron pinnatifidus A. Gray, Proc. Amer. Acad. Arts 21:386. 1886. Type: MEXICO, Chihuahua: cool, grassy slopes near Chihuahua, 19 Oct 1885, C.G. Pringle 303 (cited by Gray as Pringle 103) (holotype: GH!; isotypes: CINC!, CM!, MEXU!, MICH!, NY-2 sheets!, PH, RSA!, US-2 sheets!). Erigeron chihuahuanus E. Greene, nom. nov. Pittonia 2:169. 1891.

Achaetogeron purpurascens Greenm., Proc. Amer. Acad. Arts 39:94. 1903.

Type: MÉXICO, Chihuahua: Sierra Madre, near Colonia Garcia, 8000 ft, 27 Jul 1899, C.H.T. Townsend & C.M. Barber 175 (holotype: GH!; isotypes: MICH!,NY!,PH!,UC!,UNM-2 sheets!,US-2 sheets!). Erigeron wislizeni subsp. purpurascens (Greenm.) Nesom, Sida 9:225. 1982.

Perennial herbs with fibrous roots, from a simple caudex or short, thick rhizome. Stems 1 (2-9), erect, 25-70 cm tall, usually with 1-7 branches on the upper half, these usually with secondary and tertiary branches, moderately to densely pubescent, spreading or slightly retrorse, sometimes antrorsely appressed on the upper 1/2-1/4 or on all the stem, eglandular or essentially so. Leaves moderately arching-hispid, eglandular or essentially so; basal 1.5-15.0 cm long, oblanceolate to elliptic-oblanceolate or sometimes entire, petiolate, coarsely toothed or lobed, usually absent at flowering; cauline gradually reduced in size upwards from the basal, lobed, toothed or entire, the bases not ampliate or clasping. Heads solitary on naked peduncles 1-10 cm long, 7-12 mm wide; phyllaries 3.5-5.0 mm long with the outermost even or 1/2-2/3 as long, moderately to densely hispid-pilose, eglandular to minutely and inconspicuously stipitate-glandular, margins thick, whitish; receptacles shallowly alveolate. Ray flowers 115-180 in 2-3 series, the corollas white, blue or purple, 9.0-15.6 mm long. Disc corollas often with purple lobes, 2.2-3.0 mm long. Achenes 1.0-1.8 mm long, with 2 (3-4), thick ribs; pappus a prominent hyaline corona with an erose margin or a series of basally fused hyaline scales 0.2-0.5 mm high, ray pappus rarely with a single barbellate bristle. Chromosome number, n=9 pairs.

Chihuahua, Sonora, Sinaloa; margins, clearings or openings in oak, pine-oak, or pine woods, also common in grasslands in large basins in the north-central part of the state; 1700-2300 m; Jul-Oct. Map 7.

Representative collections examined: MÉXICO, Chihuahua: [Mpio. Madera], Chuhuichupa, Aug-Sep 1936, LeSueur 966 (ARIZ, CAS- 2 sheets, GH, LL, MEXU, PH, UC-2 sheets); Mpio. San Pablo Balleza, 5 km NE of El Vergél on Hwy 24 from Parral, 21 Aug 1981, Nesom 4468 (ARIZ, CAS, CHAPA, COLO, ENCB,F,GA,GH,GUADA,ILL,K,M,MEXU,MICH,MO,NCU,NMC,NY,OBI, OS,RM,SD,TEX,UCR,UC,US,UTEP,WAT,WIS); 10.4 km NNE of El Vergél on Hwy 24 from Parral, 23 Aug 1983, Nesom 4877 (ARIZ, CAS, MEXU, MO, NY, RSA, TEX); Mpio. Guerrero, road to San Juanito, 5 mi S of jet with Hwy 16, 23 Aug 1981, Nesom 4485 (ARIZ, ASU, CAS, COLO, ENCB, GH, MEXU, MICH, MO, NMC, NY, RM, TEX, UCR); Mpio. Guerrero, 9.8 mi W of Tomochic on Hwy 16, 17 Aug 1984, Nesom 5069 (CAS, MEXU, NMC, NY, TEX); Mpio. Temosachic, 1.5 mi E of Yepachic on Hwy 16, 20 Aug 1984, Nesom 5128 (CAS, MEXU, NMC, NY, TEX). Sinaloa: Sierra Surotato, Ocurahui, 27-30 Aug 1941, Gentry 6218 (ARIZ, CAS, GH, MICH, NY, PH). Sonora: Cerro Saguarivo, E of San Bernardo, 7-8 Aug 1935, Pennell 19609 (PH,US); Yécora, 3 Aug 1970, Pennington 92 (TEX).

Erigeron wislizeni is recognized by the following characters: fibrous roots from a short caudex or short, lateral rhizome; stems usually one from the base, few-branched from near the middle, sometimes unbranched; receptacles alveolate; and pappus a hyaline, laciniate-margined corona or series of basally fused scales, 0.2-0.5 mm high, without bristles.

I earlier viewed Erigeron wislizeni as divided into several population systems deserving taxonomic recognition (Nesom, 1980; 1982). In particular, I formally recognized the purple-rayed populations in northwestern Chihuahua as subsp. purpurascens. Also, I tentatively (1980) recognized the plants from Sierra Surotato, Sinaloa, as a distinct species.

After a great deal more field experience, however, I now perceive Erigeron wislizeni as the most variable species of sect. Polyactis and recognize no infraspecific taxa. Most conspicuously, plants of this species vary in the orientation of stem pubescence (closely appressed to spreading), leaf shape (deeply pinnatifid to entire or nearly so) and ray color (white to violet). Those with pinnatifid leaves and spreading stem pubescence are particularly common in west-central Chihuahua (see Nesom 5069; Nesom 4485 has pinnatifid leaves with linear lobes and appressed pubescence); toothed-leaved plants with appressed or variably spreading to appressed stem pubescence are most common elsewhere (see Nesom 4468, 4877 and 5128). Strongly violet-rayed plants are restricted to northwestern Chihuahua (see LeSueur 966). There is too broad a region of intermediacy in each of these characters to be able to identify varieties without an unacceptable degree of arbitrariness.

Erigeron wislizeni is very similar to E. griseus, even as Greenman recognized in the original description of the latter. Both taxa sometimes produce short, fibrous-rooted rhizomes, and both have non-clasping leaves, long, naked peduncles and a pappus without bristles. They are the only two taxa in sect. Polyactis that produce white and violet-rayed forms, and in both, the orientation of the stem pubescence is variably appressed to spreading, the leaf shape varies from nearly entire to deeply pinnatifid and there is commonly an extra, thick rib on each of the flattened faces of the achenes. In southern Chihuahua, particularly, the habit and leaf morphology of E. wislizeni closely approach those of typical E. griseus. Their geographic ranges, however, apparently are disjunct; neither has been collected in northern Durango. Morphologically, E. griseus differs (discontinuously) from E. wislizeni in its pappus reduced to a blunt rib less than 0.05 mm high (vs. a laciniate, hyaline corona 0.2-0.5 mm high) and inner phyllaries with relatively broad, hyaline margins (vs. thick, whitish margins); plants of E. griseus also average smaller in size, have a stronger tendency to produce basally ascending, unbranched stems and have punctate or weakly alveolate (vs. strongly alveolate) receptacles.

See the discussion under Erigeron rhizomactis and E. circulis for com-

ments on their relationship to E. wislizeni.

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